A REVISION OF THE ENGLISH WEALDEN FLORA, I

CHARALES—GINKGOALES

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JOAN WATSON

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A REVISION OF THE ENGLISH WEALDEN FLORA, I

CHARALES—GINKGOALES

By JOAN WATSON

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SYNOPSIS

The English Wealden flora described by Seward (1894, 1895) is here revised using modern techniques, in particular in the study of the plant cuticles. Much of the work has been carried out on the existing collections in the British Museum (Natural History), but a number of new species in the form of isolated leaf cuticles have been obtained by bulk maceration of " coaly-shales " collected by the author from the Fairlight Clay at Hastings, Sussex.

The present work covers the Thallophyta, Bryophyta, Pteridophyta, Pteridospermae, Cycadales and Ginkgoales. A second part will deal with the Bennettitales and Coniferales together with a special section devoted to a complete revision of the Wealden Equisetales.

I. INTRODUCTION

English Wealden Flora.

This work is a revision of part of the English Wealden Flora, using modern techniques. It has been carried out largely from a study of the Wealden plants in the British Museum (Natural History). Most of this material was collected from the coast in the neighbourhood of Hastings, Sussex in the latter part of the last century and belongs to the Beckles, Dawson, Mantell and Rufford Collections. The majority was collected by Mr. P. Rufford but unfortunately his specimens are merely labelled " Ecclesbourne, Nr. Hastings " and the exact localities are not recorded. Attempts were made to find fresh material along the coast between Hastings and Pett Level but unfortunately no fossils were found. However, material was obtained from coaly lenses and partings which occur in the Hastings Beds. Bulk maceration of these " coaly-shales " yielded quantities of spores, isolated leaves and even small shoots. Two of the species thus obtained are described here, including the first record of a member of the Ginkgoales from the English Wealden. Similar coaly-shales from the Wealden in the Isle of Wight yield identical plant fragments.

The flora was previously described by Seward (1894, 1895). His identifications of the fossils were based solely on macroscopic features and were figured by means of woodcuts and lithographs. A re-examination of the fossils using modern techniques shows that many of Seward's determinations are wrong. However, where the type material of a particular species (usually from the German Wealden) has not been redescribed or examined it is impossible to say if the identification is truly accurate.

Seward arranged the flora into about seventy-five species. From more than a dozen of these I was unable to get any significant new information, and unless better material is found it seems that only a redescription of their gross morphology would be possible. Most of the ferns come into this category and only a few species are dealt with here in any detail. There are very few fertile specimens available and one such fern, *Onychiopsis psilotoides* (Stokes & Webb), has recently been redescribed by Tattersall (1961). The practice of coating specimens with varnish in the past has caused the destruction of the cuticle in many specimens and has greatly hindered revision.

The Thallophyta, Bryophyta, Pteridophyta, Pteridospermae, Cycadales and Ginkgoales are described in this paper with the exception of the Equisetales. A recent find of more petrified material belonging to the Equisetales renders necessary a further revision of the species (see Watson 1964), and this will be published in a later volume together with the Bennettitales and Coniferales.

Other Wealden Floras

The Wealden floras of Germany, France and Belgium were all described in the last century in the same way that Seward described the English flora. Since then little progress has been made and work as detailed as that presented here scarcely exists. Cuticles have been described for a few species from time to time (Carpentier 1939) but the amount of work to be done remains enormous. The German Wealden flora in particular should be thoroughly revised as it contains so many type specimens. A number of English fossils are referred to German species merely on external characters. When a species under revision can only be compared with the inadequate, original nineteenth century description of the type an impossible situation arises. It has hitherto been thought that the English and German floras are more or less identical but I suspect that this may not be so. In some cases fairly recent work on foreign material has shown that a number of English specimens previously referred to German species are different from the type [*Sphenolepis kurriana* (Dunker), *Sphenolepis sternbergiana* (Dunker), *Pseudocycas dunkeriana* (Schenk)] and these were described as new species (Watson 1964). But for the vast majority of species no such comparison is possible. It is also now known that the German and English Wealden are not wholly contemporaneous (see Table I). For these reasons I feel that it is of little value to produce comparative lists of species for the various localities. This has been done frequently in the past and perhaps most recently and comprehensively by Delcourt & Sprumont (1955). Such lists, however, are probably highly inaccurate and will remain so until there is a wholesale revision of all Lower Cretaceous fossil floras.

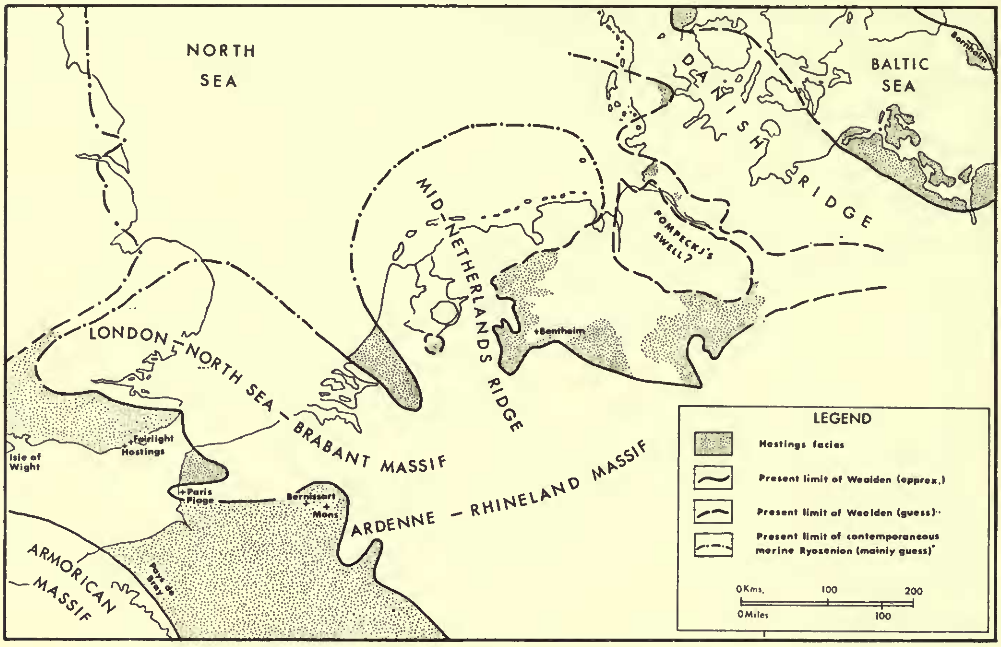


FIG. 1. Inferred present extent of Wealden strata. (After Allen 1967)

Techniques

Techniques used were of the simplest. With few exceptions the usual method for bulk macerations was used (see Harris 1926).

Stratigraphical background

The stratigraphy of the Wealden has been described by White (1928), Allen (1954, 1955, 1959, 1960, 1965, 1967), Hughes (1958) and Howitt (1964). Owing to its alleged relict fauna and flora of Jurassic affinity the English Wealden has on occasions been assigned to the Jurassic System. It is now, however, generally

	TETHYAN	BOREAL			
	South-east France	North-west Germany		Southern England	
CRETACEOUS (part)	Barremian	Barremian		Weald Clay	CRETACEOUS (part)
	Hauterivian	Hauterivian			
	Valanginian	'Upper & Middle Valdensis'		Hastings Beds	
	Berriasian	'Wealden'	PURBECK	Durlston Beds	
		Upper Serpulite			
		Lower Serpulite		Lulworth Beds	JURASSIC (part)
		Münder Marls		Portland Beds	
JURASSIC (part)	Tithonian	Eimbeckhausen Plattenkalk			

TABLE. 1—Correlation of N. W. European " Wealden " (from table 4 in Dodson, Rex, Casey & Allen 1964).

accepted as part of the Cretaceous. Part, or even all, of the Purbeck might also be Cretaceous. Table I is a correlation table for the Wealden of north-west Europe recently proposed by Dodson, Rex, Casey & Allen (1964). On the basis of glauconite studies the radiometric age of the Jurassic/Cretaceous boundary is estimated to be about 135 million years. Text-fig. 1 shows the present extent of the Wealden.

The Fairlight Clays have yielded most of the fossil plants, particularly in the region of Ecclesbourne Glen. The large number of specimens collected by Mr. P. Rufford and others has led to the false impression, which has been perpetuated (Gallois 1965), that plants are abundant in the Fairlight Clays. This is not so: even small fragments are quite rare. It has not been possible to ascertain the exact localities and horizons at which Rufford collected; nor is it known over what period of time the collection was assembled. In a brief description of the Hastings Beds by Rufford (Seward 1894 : xvii) he refers to the Fairlight Clays " yielding, very locally, Ferns, Cycads and Conifers " and also to " the very limited extent of outcropping fossiliferous strata ". In the early years of this century (around 1910) a further important collection of Wealden plants was made by P. Teilhard de Chardin and Felix Pelletier, two Jesuit priests who stayed in the area for four years. Their specimens (Seward 1913) were collected mainly in the neighbourhood of Fairlight which is about a mile to the east of Ecclesbourne Glen. The collection was subsequently divided between the British Museum (Natural History) and the Hastings Museum. The Hastings Museum also has a large number of Rufford's specimens, many of which are the counterparts of the specimens in the British Museum (Natural History). Attempts at collecting in recent years have yielded nothing to compare with the magnificent specimens (fronds three feet long) obtained by these earlier collectors.

ACKNOWLEDGEMENTS

This work forms part of a Ph.D. thesis of the University of Reading, supervised by Professor T. M. Harris, F.R.S. and I thank him for his unfailing patience, kindness and encouragement. I wish also to thank Professor P. Allen for much help and for permission to reproduce his text-figures.

Some of the work was carried out in the Department of Palaeontology, British Museum (Natural History), some in the Botany Department, University of St. Andrews and some in the Herbarium, Manchester Museum where I was given research facilities for which I am most grateful. Thanks are due to the Keeper of Palaeontology, British Museum (Natural History) for permission to work on the collections.

Tenure of a D.S.I.R. Studentship is gratefully acknowledged.

II. SYSTEMATIC DESCRIPTIONS

Unless otherwise indicated in the text all specimens are in the collections of the British Museum (Natural History) and are prefixed by V.

THALLOPHYTA

CHLOROPHYCEAE. CHARALES

Organ Genus ***CIRCONITELLA*** nov.

DIAGNOSIS. Gyrogonite uncalcified, cutinised; surrounded by five sinistrally spiralled cells; shape ellipsoidal, circular in transverse section. Apical pole formed by all five cells; basally ending against a basal plate; without basal cage.

TYPE SPECIES. *Chara knowltoni* Seward 1894; 13, Text-fig. 1.

DISCUSSION. This genus is recognized for the type species which was formerly included in *Nitellites* Horn af Rantzien in my Ph.D. thesis of 1964. The diagnosis of *Nitellites*, however, requires that size and shape should be very close to that of the

Recent genus *Nitella* but *C. knowltoni* differs in being somewhat larger and unflattened.

Dijkstra (1959) describes an uncalcified gyrogonite which he refers to as "*Praechara symmetrica* Peck cf.". I am satisfied, from his diagnosis and photographs that this fossil is identical with *C. knowltoni* (Seward). Whilst this species fits into *Praechara* Horn af Rantzien (1954) on its general shape and apical structure, *Praechara* has hitherto been used only for members of the Characeae, i.e. calcified gyrogonites which cannot be placed in other well-defined genera.

Circonitella knowltoni (Seward) comb. nov.

Pl. 1, figs. 1–5; Text-figs. 2–6.

1894 *Chara knowltoni* Seward : 13, text-fig. 1.
1959 *Praechara symmetrica* Peck cf.; Dijkstra : 15, pl. 2, figs. 20–23.

EMENDED DIAGNOSIS. Gyrogonite uncalcified, ellipsoidal in side view, apical and basal halves similar, 400μ to 665 μ long and 380 μ to 550 μ wide. Spiral cells five, sinistrally spiralled, about 45 μ wide near equator and showing about twelve convolutions laterally. Cells usually slightly concave with distinct intercellular ridges 3 μ to 15 μ wide, sometimes flat and occasionally convex. Outer cutinised membrane (ectosporostine of Horn af Rantzien) marked with coarse but very low and ill-defined tubercles up to 5 μ diameter. Inner membrane (endosporostine of Horn af Rantzien) present, delicate and without a patterned surface. Apical pole formed by ends of spiral cells meeting in a slightly eccentric pattern; basal pole with rounded plate 100 μ wide; no cage or basal claws present.

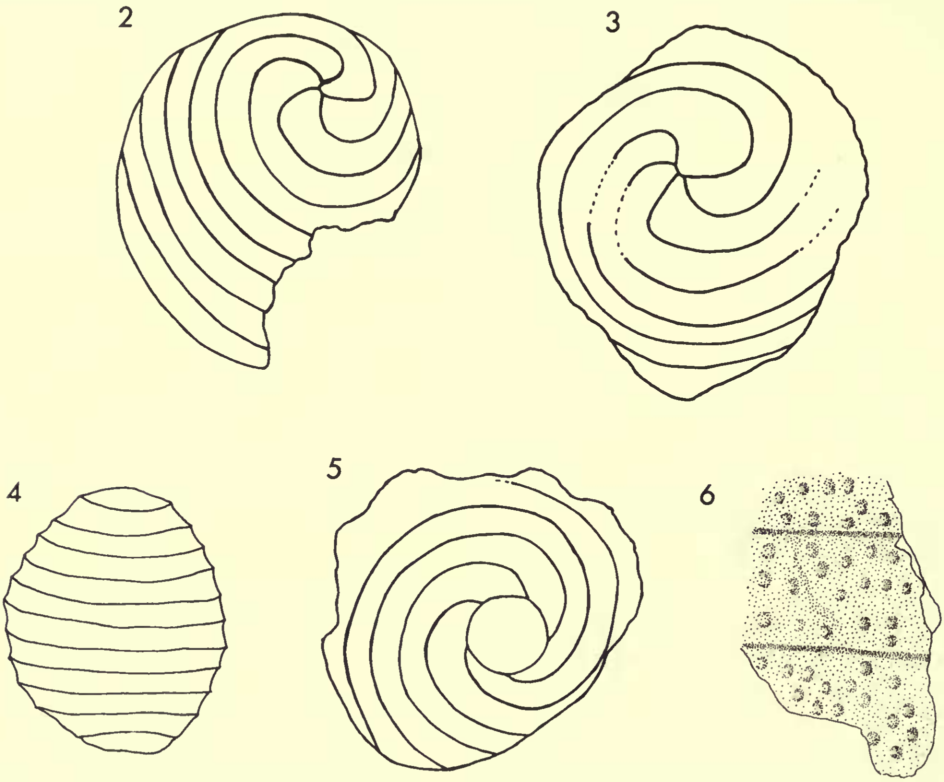
NEOTYPE. V.51555.

DESCRIPTION. Numerous black cutinized gyrogonites are embedded in an argillaceous matrix, the majority being flattened and presenting a lateral view but a few being orientated so as to show polar views. A few gyrogonites preserved by pyritization are completely unsquashed and were obtained by macerating small pieces of the rock in water. These specimens show that the gyrogonite was originally completely circular in section and that flattening occurred during preservation. Whereas most of the flattened specimens have concave spiral cells with intercellular ridges the solid ones have convex spirals with depressions between and tend to be somewhat larger. However, one of them (V.51555) has part of the convex surface broken away revealing the familiar concave cells with ridges below. These two surfaces are interpreted as the outer and inner walls of the spiral cells.

Apical poles are not seen nearly so frequently as basal poles but a few undistorted specimens were obtained. It may be noted that in the material from the Netherlands, Dijkstra (1959) also found the apical poles of the gyrogonites less well preserved. The tips of the spiral cells tend to be swollen and meet in a slightly irregular pattern. Many more basal poles are seen with the easily identifiable circular plate against which the five spiral cells end in a regular manner. Their width near the pole is the same as at the equator.

Laterally up to twelve convolutions of spiral cells are seen each making more than two turns. Thus the spiral is so flat that the furrows and ridges appear almost horizontal. As mentioned above the spiral cells are concave in most gyrogonites but convex in a few specimens. There are also many in which they are flat and their margins are then nearly, or quite, invisible in the untreated fossil. For variety in intercellular ridges compare Pl. 1, figs. 2, 4.

The tubercles on the ectosporostine are irregularly arranged about $8\ \mu$ apart, usually about four tubercles across the width of a spiral cell. Many gyrogonites gave no satisfactory cuticles at all and some that did yield cuticles were less clearly marked. The cuticle is usually reddish-brown in colour but in parts the inner membrane of the wall is seen alone as a straw-coloured homogeneous layer without markings of any kind. The coronula is not known, nor is the oospore.



Figs. 2–6. *Circonitella knowltoni* (Seward). 2, 3. Gyrogonites showing apical pole. Fig. 2, specimen accidentally destroyed. Fig. 3, V.51549. × 100. 4. Side view of a gyrogonite with concave cells, showing the very flat spiral. V.51550. × 75. 5. Basal pole of a gyrogonite. V.3114. × 100. 6. Cutinized wall showing part of three spiral cells with tubercles on the outer layer. The inner layer of the wall is seen on the right of the middle cell. Slide V.51551. × 350.

Dijkstra suggested that his fossils were originally calcified but became decalcified during preservation. It is much more likely, however, that the present specimens were never calcified. There is evidence that both the concave inner wall and the convex outer wall of the gyrogonite cells are composed of organic matter and if my interpretation of these layers is correct then it seems conclusive. It is clear that in the specimens with only the inner organic layer present the fine clay matrix is everywhere pressing against this layer; there is no gap at all such as would be left if a lime-shell had been dissolved. We would have to suppose that decalcification occured first, then preservation. This species is preserved in a unique way in specimens from two widely separated localities and it seems unlikely to have been caused by the same unusual event at two distant places.

The absence of a calcareous shell on the outside of the gyrogonite immediately suggests Nitellaceous affinities but further study shows that in other features it is more like the Characeae. I make no assumption about the correct classification of the plant producing this gyrogonite.

In all the Nitellaceae the gyrogonites are laterally compressed whereas *Circonitella knowltoni* is quite round in transverse section as are members of the Characeae. In studying a number of living Nitellaceae, Horn af Rantzien (1959) found *Nitella hyalina* to be the least flattened, a typical specimen being 340 μ long, 260 μ wide and 180 μ thick. He also gives details concerning the average size of *Nitella* gyrogonites: '. . . generally speaking the oosporangia (gyrogonites) of *Nitella* are small, in most species the length does not exceed 350 μ'. *C. knowltoni* is much larger, attaining almost twice this length, although *Nitella* gyrogonites with larger dimensions do occur, e.g. *N. flexilis* which reaches 575 μ long (Groves & Bullock-Webster 1917).

Twelve convolutions of spiral cells seen in lateral view is common in the Characeae but in the genus *Nitella* the largest number known is eleven, in *N. polygyra*. A more usual number in this group is five or six and hence the angle of the spiral is steeper than in *C. knowltoni*.

Amongst British Charales the most similar ectosporostine pattern is seen in *N. opaca*, although the tubercles are more numerous and larger. Most of the Characeae have a much smoother granulate surface. The absence of basal claws accords with Recent species of *Nitella*.

Apart from Quaternary fossils the only other uncalcified gyrogonites are *Nitellites sahnii* Horn af Rantzien and *Nitellites* sp. (Horn af Rantzien 1957) from the Middle to Upper Jurassic Rajmahal series of India. Both differ from *C. knowltoni* in having more in common with the Recent genus *Nitella*. They are much smaller, being only 160 μ at the longest, and they are laterally compressed. The spiral cells show only six to eight convolutions and the ectosporostine has a reticulate surface.

Genus ***GYROGONA*** Lamarck

Gyrogona medicaginula Lamarck

Selected references-

1804 *Gyrogona medicaginula* Lamarck : 355.
1829 *Chara medicaginula* (Lamarck); Lyell : 91, pl. 13, figs. 1–8.
1933 *Gyrogona medicaginula* Lamarck; Groves : 24, 25, 39.
1965 *Gyrogona medicaginula* Lamarck; Grambast & Paul : 239, pl. 1, figs. 1–4.

Remarks. Several gyrogonites of this species are present in a piece of pure siliceous rock (V.2928) which is included in the Wealden Collections (British Museum, Natural History). The specimen has the appearance of a large pebble from the beach and it seems probable that it is not Wealden in age. *G. medicaginula* is otherwise only known from the Tertiary (Lyell 1829, Grambast & Paul 1965) and is found in the Oligocene of the Isle of Wight. The specimen is accompanied by a note written by Groves and is probably the specimen to which he refers (Groves 1933 : 25) when saying " Fruits collected from a Wealden deposit, Fairlight Glen, Hastings (Sussex), England . . . are considered by the present writer to be referable to this species ".

The matrix cannot be matched to anything in the Hastings Beds and the gyrogonites of *G. medicaginula* are much larger than is usual in pre-Tertiary species. It seems probable, therefore, that the specimen was mistakenly identified as Wealden; perhaps washed-up on the beach near Hastings.

BRYOPHYTA

MUSCI

? *Bryophyte* leaf.

Text-figs. 7–9

Leaf elliptical, nearly 2 mm. long, just over 1 mm. wide. Margin entire, one end (possibly both) rounded. No midrib present. Lamina flat, one cell thick, cells forming about eight longitudinal rows, marginal cells smaller, about as long as broad. Cell walls thin, not locally thickened at corners; no surface thickenings observed.

Material. V.2857, V.2857*a*, V.2857*b*.

This small fossil is known from three isolated specimens which are very similar; one has a counterpart. The above description assumes it is like a Bryophyte leaf but I have been unable to find a Bryophyte leaf with similarly arranged cells. In the leafy liverworts the cells tend to be isodiametric or rounded and do not form longitudinal rows. In *Naiadita lanceolata* Buckman (Harris 1938) the cell rows are markedly transverse. In the mosses they are isodiametric to elongated but they may form longitudinal rows. Transversely elongated cells are very rare in mosses but they are seen in a few *Tortula* species. However they have leaves which are otherwise different.

Ventral scales and rounded appendages of the scales of the Marchantiales have more or less elongated cells and where rows are recognizable they are transverse, never longitudinal. In fern ramenta the cells are often in longitudinal rows but are usually very narrow.

HEPATICAE

The fossils described here are all thalloid and branch dichotomously and some of them form a rosette-like growth. Some show definite Hepatic features rather than Algal, but others do not, although they look like Hepatics. Various generic names have been used for such fossils by earlier authors (e.g. *Marchantites* Brongniart) suggesting rather precise affinity. Walton (1925) in giving fine details of such fossils for the first time revised their classification. A fossil with definite Hepatic features he called *Hepaticites*. This feature in practice is usually the presence of rhizoids. Fossils in which no rhizoids were demonstrated he called *Thallites*. According to this scheme the genus *Marchantites* is now restricted to forms showing definite Marchantialean characters. Thus *Marchantites zeilleri* Seward was referred to the genus *Thallites* Walton (Harris 1942). Further study of this plant has revealed the presence of rhizoids and it is here included in *Hepaticites* Walton.

Lundblad (1954) separated from *Hepaticites* those species showing Marchantialean ventral scales as *Marchantites* and those with Marchantialean air-chambers as *Marchantiolites*. In the present work the two genera of Walton suffice, but one species which almost certainly has Marchantialean ventral scales would have been placed in *Marchantites* had it been well enough preserved for the facts to be secure.

Genus ***HEPATICITES*** Walton 1925 : 565

Hepaticites zeilleri (Seward) comb. nov.

Pl. 2, figs. 1–3

1894 *Marchantites Zeilleri* Seward : 18, pl. 1, fig. 3.
1942 *Thallites zeilleri* (Seward) Harris : 397.
1954 *Thallites zeilleri* (Seward); Lundblad : 408.

EMENDED DIAGNOSIS. Plant thalloid, dichotomously branched, distance between dichotomies not constant. Thallus about 3 mm. broad, composed of dark, well defined midrib 1 mm. wide and delicate lamina probably one cell thick. Margins entire. Cells of thallus in rows, longitudinal in midrib but inclined at an angle of about 45° in lamina; cells about 30 μ wide. Near apex midrib tending to divide into number of divergent dark bands separated by thinner tissue. Numerous unicellular thin walled, non-tuberculate rhizoids arising on midrib, up to 5 mm. long and typically 40 μ wide.

HOLOTYPE. V.2330.

DESCRIPTION. The holotype suggests a rosette shaped thallus in the position of growth (Pl. 2, fig. 1 shows the counterpart). A second specimen shows smaller pieces of thallus mixed with fragments of *Onychiopsis* and is more likely to have been deposited by water.

The thallus branches are delicate towards the tip and the apex is nowhere visible. Here the midrib is more delicate and seems to divide. In this delicate part longitudinal rows of cells can be seen but elsewhere the midrib is very dark and opaque and presumably several cells thick. The rows of cells in the lamina are clearly seen only in a few places and then only the longitudinal walls are preserved.

There is nothing suggesting Marchantialean air chambers or ventral scales. The rhizoids although clear are only moderately well preserved, unbranched and without septa; their walls appear to be plain rather than tuberculate. They form groups arising from the midrib and usually point forwards. A number of detached rhizoid bunches are present beside the thallus.

COMPARISON. *H. zeilleri* is the only British Wealden liverwort with a clearly defined midrib and lamina. Among other fossils it bears a most striking resemblance to *H. laevis* Harris (1931) from the Lower Lias of East Greenland. The rows of cells in that species are more clearly defined and the midrib is 0·5 mm. wider than in *H. zeilleri* but otherwise they look the same.

Other similar species are: *H. arcuatus* (Lindley & Hutton) Harris (1942 : 394, 1961 : 7) which is of similar dimensions and has a well defined midrib, but the lamina is three cells thick, and there are fewer rhizoids. *Thallites yabei* (Kryshtofovich 1932, 1938, Oishi 1940, Harris 1942) is a larger plant of which no microscopic details are known.

CLASSIFICATION. *H. zeilleri* looks very like *Pellia* and agrees with it in the cell-rows of the lamina and in the rhizoids. Plants of the *Pellia* form are familiar in the Jungermanniales anacrogynae but scarcely occur in other groups and accordingly *H. zeilleri* is placed here.

Hepaticites ruffordi sp. nov.

Pl. 2, figs. 4, 5

DIAGNOSIS. Thallus branched dichotomously at intervals of about 1 cm., width about 3–4 mm. Margins entire, apex probably notched. Greater part of thallus marked with grooves (considered to be ventral scales) at intervals of 0·5 mm. Grooves strongly arched, longitudinal in middle region but curving outwards and then slightly backwards at their ends. Middle region of older part of thallus, about 2 mm. wide, marked by two lines appearing thicker and beyond which grooves do not extend.

HOLOTYPE. V.2343.

DESCRIPTION. The only specimen known is preserved as an impression in fine sandstone; a little of the plant substance remaining as a dark stain but this has cracked and no cells are seen satisfactorily. Faint marks crossing the grooves may be the impression of cells but there is nothing more. No rhizoids were seen nor any structure in the lamina. *H. ruffordi* is tentatively placed in *Hepaticites* because it is thought to show a distinctive Hepatic character—ventral scales—even though rhizoids are not preserved. These ribs, or ventral scales, are of interest since they are confined to the Marchantiales. Unfortunately the specimen is too poorly preserved to be sure that they are indeed scales. I have, therefore, refrained from including it in *Marchantites* in Lundblad's sense.

COMPARISON. *Marchantites hallei* Lundblad (1955) is a liverwort from the Lower Cretaceous of Patagonia. It is similar in dimensions to *H. ruffordi* but is known in much more detail, having two sorts of rhizoids and well preserved ventral scales. *Hepaticites haiburnensis* Harris (1961 : 9) is another similar form in which the thallus extends further beyond the scales.

Genus ***THALLITES*** Walton 1925 : 564.

For discussion of *Thallites* see p. 219. The two species described here are associated in considerable numbers on certain bedding planes. Seward placed them in

Algites thinking them to be marine red algae. Closer study shows that they are more likely to be terrestrial liverworts though proof is lacking. They are certainly not marine for the rocks in which they occur are of purely freshwater origin and indeed the specimens are crowded with the small freshwater lamellibranch, *Neomiodon.* Despite careful study the two forms described here show so few details that they can hardly be considered to be properly characterized species. However, they have been described as such and as their names are fairly well known they are here retained.

Thallites valdensis (Seward) comb. nov.

Text-figs. 12–15

1894 *Algites valdensis* Seward : 4, pl. 1, figs. 1, 2.

EMENDED DIAGNOSIS. Plant thalloid; thallus forming rosette of segments branching dichotomously three or four times. Diameter of whole thallus up to 5·5 cm.; width of branches typically 4–5 mm., branches ending bluntly. Midrib represented by median dark line 100 μ wide and dichotomizing 5 mm. behind dichotomy of thallus. Cells in midrib region not differing from rest of lamina. Dark ribs passing obliquely across lamina at intervals of about 300 μ. Lamina apparently composed of one layer of thin walled cells ranging in size from about 15–75 μ.

HOLOTYPE. V.2857.

DESCRIPTION. Seven specimens were examined on three blocks of fine-grained calcareous sandstone. The preservation is poor and splitting of the rock has resulted also in splitting of the fossil into two parts. The rosette of branches strongly suggests that the plant has been preserved in position of growth. It accords with a suggestion made by Walton (1949) for a Carboniferous thallus which he called cf. *Hepaticites*. Like Walton's specimen there are several very perfect rosettes and it looks as though the central and oldest part of the thallus had decayed away before the plants were buried and preserved. Fragments would be unlikely to drift together into a neat rosette.

The general appearance of the cells is constant throughout the whole thallus though they vary considerably in size and shape. They are on the whole thin walled but additional organic material is present which tends to conceal their walls. The positions of the median line of the thallus and the ribs are merely marked by a greater concentration of this dark structureless matter. The central strand is at best faint and is clear in only two thallus branches. The rest show no central strand at all. The oblique ribs though not always seen are more widespread. I think that the pattern of cell-like polygons represents true cells and is not some effect of poor preservation, for instance the imprint of sand grains on a thin coaly layer. At best they certainly look like cells and associated with *T. valdensis* are small fragments of equally delicate plant tissue, also one layer thick but with quite differently shaped cells. One of these fragments is the small leaf described here as ?Bryophyte leaf; another is more like a fern ramentum with very narrow cells. In neither is there any possibility that the cellular pattern has been imposed by sand grains.

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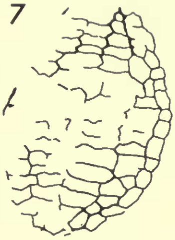

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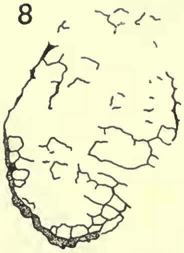

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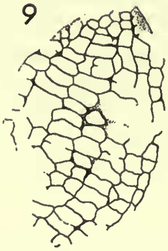

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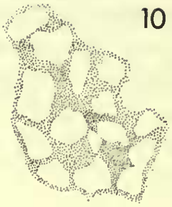

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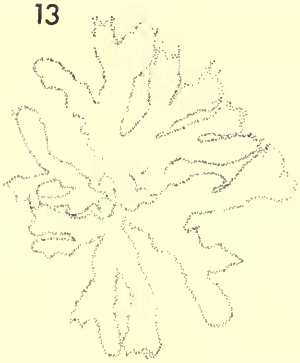

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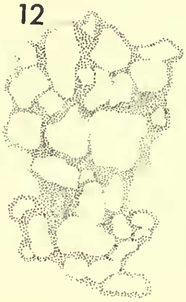

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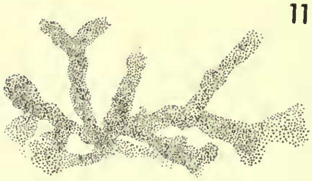

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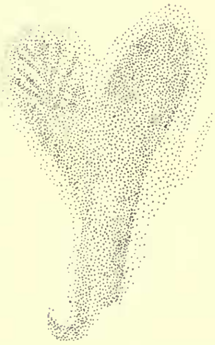

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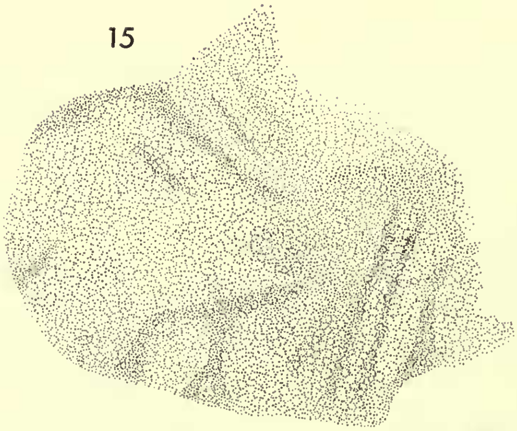


Figs. 7–9. (?) Bryophyte leaf. 7, 8, 9. Leaf showing a single layer of cells. Figs. 8, 9 are part and counterpart. Fig. 7, V.2857*b*. Figs. 8, 9, V.2857. All × 20.

Figs, 10, 11. *Thallites catenelloides* (Seward). 10. Part of specimen showing cells. V.2857. × 100. 11. Part of thallus. V.2857. × 4.

Figs. 12–15. *Thallites valdensis* (Seward). 12. Part of specimen showing cells. V.2857. × 100. 13. Rosette shaped thallus suggesting preservation *in situ*. V.2857*b*. × 1. 14. A branch of the thallus showing thinner peripheral region and ribs of the thicker central region. V.2857*b* × 4. 15. Apex of branch showing the pattern of divergent ribs. V.2857*b*. × 15.

No Marchantialean air chambers are visible, nor is there any clear suggestion of two superimposed layers of cells, though presumably further layers do occur, at least on the midrib and lateral ribs. No rhizoids are present.

Transfers were made but these yielded no additional information. *Chondrus crispus*, the red alga with which Seward compared T. *valdensis* was found to be quite unlike it in having a much thicker thallus and cells of very different shape.

COMPARISON. *T. catenelloides* has a thallus of similar texture but is a much smaller plant. Of the other British Wealden forms *Hepaticites zeilleri* differs in its clearly marked midrib and strong rhizoids. *H. ruffordi* differs in its strong pattern of arcuate ribs.

Most thalloid liverwort-like plants have a broad and strongly marked midrib. The following which are of similar dimensions to *T. valdensis* have only a faint midrib.

T. uralensis Kryshtofovich & Prynada (1933) from the Rhaeto-Liassic of U.S.S.R. is rather narrower and has more pointed lobes. No microscopic details are known.

Hepaticites rosenkrantzi Harris (1931, 1937) from the Lower Lias of East Greenland has no midrib but is two cells thick, the cells tending to be elongated and in rows.

H. amauros Harris (1937), also from the Lower Lias of East Greenland, has a midrib which is a dark, narrow strip but the thallus is many cells thick.

Thallites catenelloides (Seward) comb. nov.

Text-figs. 10, 11

1894 *Algites catenelloides* Seward : 7, pl. 1, figs. 1, 2.

EMENDED DIAGNOSIS. Plant thalloid; thallus dichotomously branched, branches about 0·5 mm. wide; margins probably entire. Thallus composed of uniform tissue one cell thick; cells thin walled, diameter about 50 μ.

HOLOTYPE. V.2857.

DESCRIPTION. Numerous specimens occur on the same blocks as *T. valdensis* and in some cases they are closely associated. The specimens of *T. catenelloides* vary from small fragments to what are probably whole thalli measuring 1 cm. across. They do not form rosettes. The narrow ribbon-like thallus branches frequently and in parts appears to have an undulating though entire margin. The specimen in Text-fig. 11 is the same as that figured by Seward. His suggestion that the thallus has constrictions similar to the red alga *Catenella* seems to be based only on the appearance of part of this particular thallus. It is not seen in the other specimens and is probably due to the undulating margin.

The cells of the thallus are identical with those of *T. valdensis* and the description for that species will serve for both. Transfers were made but these showed only the single layer of cells composing the thallus.

COMPARISON. In *Catenella opuntia* the thallus is several cells thick and has a surface layer of cells much smaller than those of *T. catenelloides*, whilst the central cells are larger and elongated.

All other Mesozoic hepatics, including the three other English Wealden species, are much larger than *T. catenelloides*. The only plants of similar dimensions are from the Carboniferous. Two rather similar fossils are *Thallites willsi* Walton (1925, 1928, 1949) and *Hepaticites langi* Walton (1928). Neither has a definite midrib, both differ in being more than one cell thick and *H. langi* has well marked rhizoids. *T. willsi* which is more comparable has a rather broader thallus.

PTERIDOPHYTA

LYCOPODIALES

SELAGINELLACEAE

Genus *SELAGINELLA* Spring

Only one other *Selaginella* from the Mesozoic, *S. hallei* Lundblad (1950*a*), is known in as much detail as the Wealden species described below and referred here to the living genus.

The genus *Selaginellites* Zeiller (1906) was originally used for heterosporous fossils having more than four megaspores in each megasporangium and was thought to differ in this respect from the Recent genus *Selaginella*. Subsequently it was used by Halle (1907) for all heterosporous fossils regardless of the number of megaspores. Later work proved that living species may produce more than four megaspores in each megasporangium (Duerden 1929). Miner (1932) used *Selaginellites* for isolated megaspores which would ordinarily have been called *Triletes* but Harris (1935) recommended that its use should be restricted to fossil shoots which showed evidence of being closer to *Selaginella* than any other genus. Dijkstra (1949) was the first to place the English Wealden species in *Selaginella* but this may have been inadvertent as he later returned to the use of *Selaginellites* without comment. I consider that the Wealden species in no way differs from a typical anisophyllous *Selaginella* with the normal number of four megaspores in each megasporangium and it has, therefore, been referred to the living genus.

Selaginella dawsoni (Seward)

Text-figs. 16–24

1894 *Plantae incertae sedis* Seward : 20, pl. 1, figs. 8, 9.
1913 *Selaginellites Dawsoni* Seward : 87, text-fig. 1.
1913*a* *Selaginellites Dawsoni* Seward; Seward : 86, pl. 4, figs. 1–7.
1949 *Selaginella Dawsoni* (Seward) Dijkstra : 19. (name in list).

DIAGNOSIS. Fertile, dichotomously branched shoots; sterile portion of shoot in part known about 1 mm. wide, dorsiventral, covered with small overlapping leaves. Leaves anisophyllous, in four ranks; leaves of upper two rows alternating and appressed to stem; rhomboid in shape, about 0·5 mm. long; leaves of lower two rows longer, probably about 1 mm. long, slightly spreading laterally but pointing towards apex. Strobilus terminal, unbranched, 2 mm. wide, at least 3 cm. long. Overlapping sporophylls decussately arranged, apparently all alike and longer than leaves, about 1·5 mm. Sporangia more or less rhomboid in outline about 0·5 mm.

across. Megasporangia fewer but distributed throughout length of strobilus; each containing four megaspores. Megaspore with rounded dorsal surface, ventral surface formed by three flattened contact facets; diameter 285 μ–340 μ (mean 306 μ); height about 15 % less; tri-radiate ridges very broad, about 30 μ high, edge rounded, not divided; length equal to radius of spore; arcuate ridges absent. Ventral surface crowded with tubercles, circular or oblong and 5–12 μ across; tubercles also present on surface of tri-radiate ridges but less prominent. Dorsal surface of spore having a coarser pattern of widely spaced ribs, irregular in shape, about 4 μ wide and up to 60 μ long; spore surface smooth between ribs. Spore wall easily separable into two distinct layers, outer 20–30 μ thick, inner about 2 μ thick. Inner membrane straw-coloured and indistinctly marked with small pits. Substance of wall, including tubercles and ribs, light brown in colour and composed of minute granules.

Microsporangia contain numerous microspores which are almost spherical but with flattened contact facets; average diameter 45 μ (range 38-52 μ); tri-radiate mark fine but distinct, equal to about two thirds of spore radius. Contact facets seen as three lobes separated by tri-radiate marks not quite reaching notches between lobes; surface of facets more or less covered with indistinct tubercles, 1–2 μ in diameter. Spore wall distinctly two layered, together only about 2 μ thick at facets but 5–6 μ thick elsewhere. Outside facets both layers uneven in thickness; inner layer becoming thicker opposite a thin place in the outer. Maximum thickness of inner layer about 3 μ, outer about 5 μ.

HOLOTYPE. V.2328.

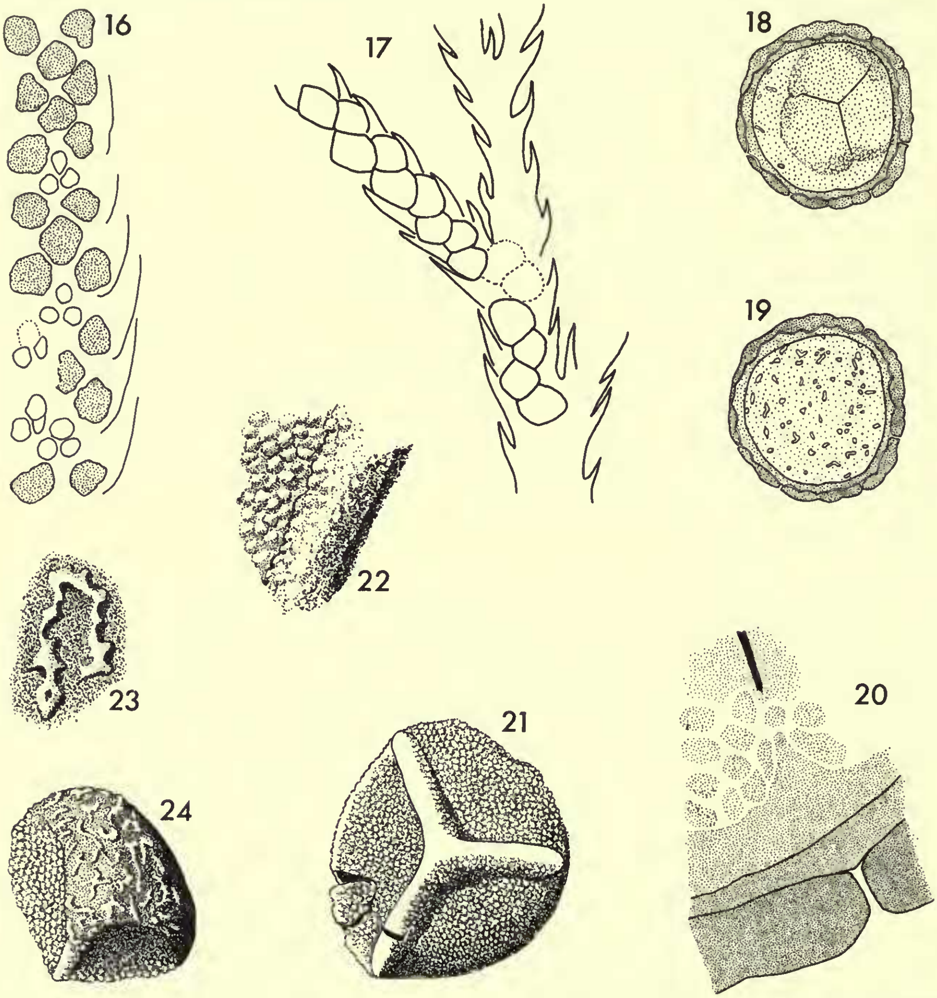
DESCRIPTION. The only material available consists of two fragments of shoot and a few lengths of cone which are present on two blocks of ironstone. Some of the cone specimens have been much damaged. The two shoots are each about 3 cm. long and frequently branch dichotomously. For the most part the sterile portion of the plant is seen merely as a faint outline on the rock, the stem and some of the leaves being replaced by a white mineral and scarcely any carbonaceous plant material remains. On only one or two branches can the phyllotaxis be worked out. Here the mineralized outlines of the dorsal leaves are seen in surface view and the ventral leaves in side view. This is the portion of shoot seen in Text-fig. 17. Although the margins of the leaves are shown as entire it is impossible to tell whether they are correctly represented since the precise margins are unrecognizable. All that is known of the shape of the ventral leaves is from what they show in side view. They are seen to have thicker tissue in the centre. The exact arrangement of the dorsal leaves just behind a dichotomy is uncertain.

The most complete strobilus is 3 cm. long but is probably incomplete, ending as it does, very sharply at the edge of the rock. Although this strobilus does not have any attached sterile part, each of the two shoots have bases of similar strobili attached to one of their branches. Three portions of cones lying close to one another and parallel indicate that a number of them were borne terminally on the plant.

The sporangial walls are not preserved though the outlines of the microspore masses are clearly seen. Only one tetrad of megaspores is present in the megasporangium.

The sporophylls are seen only at the periphery of the strobilus in side view, their general shape being unknown.

Slides of detached spores prepared by Dr. W. Chaloner and kindly lent by him show in most of the megaspores the two very distinctive ornamentations of the



Figs. 16–24. *Selaginella dawsoni* (Seward). 16. Part of a strobilus with microsporangia, megaspores in outline and sporophylls in side view. V.3151. × 10. 17. Part of a sterile shoot showing anisophylly. Holotype, V.2328. × 10. 18. Ventral surface of microspore showing contact facets, tri-radiate marks and two-layered wall in optical section. V.3151*e*. × 500. 19. Dorsal surface of the same spore. V.3151*e*. × 500. 20. Detail from the same spore showing tubercles on contact facets. V.3151*e*. × 2500. 21. Ventral face of megaspore. Specimen lost. × 100. 22. Detail of megaspore showing broad tri-radiate ridge and facet with tubercles. V.3151*y*. × 250. 23. Single rib from dorsal surface of megaspore. V.3151*y*. × 250. 24. Megaspore in side view showing dorsal surface, two facets and a tri-radiate ridge. V.3151*y*. × 100.

different surfaces and a number of broken specimens show the two separate layers of the spore wall. The thin inner layer is easily removed and mounted in glycerine jelly without further treatment. Very brief maceration of the the thick outer coat renders it transparent before mounting. Some of the megaspores do not show the two distinctive sculptures quite so clearly as the figured specimens. In these the dorsal ribs are not so coarse and well defined. Lack of abundant material prevents more detailed study of this variation.

Some of the mounted microspores remain in tetrads but most of them occur singly. The layers of the wall are clearly seen in optical section, their irregular adjacent surfaces closely interlocking, the one being at its thickest where the other is thinnest. The pits in the outer wall while most numerous on the dorsal side also occur on the ventral side but not on the facets.

By squashing the spores the thin walled facets may be detached and their surface more easily studied. In some specimens the tuberculate pattern covers the whole surface of the facet but is only marginal in others.

COMPARISON. Only one other Mesozoic *Selaginella* shoot with cone has been described, namely *S. hallei* Lundblad (1950*a*) from the Rhaetic of Sweden. The sterile shoot is similar in size but with slightly larger and more spreading leaves. Like *S. dawsoni* it is anisophyllous, but the leaves are known in more detail. The strobilus of *S. hallei* is much shorter and has sporophylls which are described as spirally arranged but may equally well be described as in alternating whorls of about four. There are four megaspores in each megasporangium. *Selaginellites polaris* Lundblad (1948) is a Selaginelloid cone from the Trias of Greenland. It is much stouter than *S. dawsoni* (7 mm. wide) and has numerous megaspores in each megasporangium.

Selaginella dichotoma Velenovsky (1931) is a sterile shoot from the Cretaceous of Bohemia with more spreading leaves.

Selaginellites nosikovii Kryshtofovich & Prynada (1932) is a sterile shoot from the Jurassic of Siberia which also has larger, more spreading leaves than *S. dawsoni*.

Among living species *S. sanguinolenta* is very similar in size and leaf arrangement, but the spores are different the megaspores being of similar size but with much more prominent tubercles on the dorsal surface.

S. emmeliana possesses strikingly similar megaspores to those of *S. dawsoni* with the same shape and sculpturing both on the dorsal and ventral surfaces. *S. emmeliana*, however, possesses other megaspores which show a great deal of variation both in size and surface ornament. Not all have different dorsal and ventral patterns, some having the coarse ribbed pattern on both surfaces whilst others have the fine tuberculate pattern on both. The foliage of *S. emmeliana* is quite different from that of *S. dawsoni*.

EQUISETALES

Genus *EQUISETITES* Sternberg

REMARKS. The external morphology of *E. lyelli* has been fully described by Allen (1941). Additional information about this species (Watson 1964) was obtained from some petrified fragments found by Mr. P. Whybrow (British Museum, Natural History). Very recently Mr. Whybrow has found much more extensive petrified material and in addition new compression material is available with easily prepared cuticle. It will, therefore, be necessary to make a complete revision of the species using all available material, including that described by Allen (1941).

Descriptions of all three species of Wealden *Equisetites* (Seward 1894) will be included in a later volume.

FILICALES

Family ***MATONIACEAE***

Genus ***MATONIDIUM*** Schenk 1871 : 219

Matonidium goepperti (Ettingshausen)

1852 *Alethopteris goepperti* Ettingshausen : 8, pl. 7, fig. 7.
1894 *Matonidium Göpperti* (Ett.); Seward : 63, text-figs. 7, 8.
1913 *Matonidium goepperti* (Ett.); Seward : 89, text-fig. 2C, pl. 14, fig. 3a.
1961 *Matonidium goepperti* (Ett.); Harris : 112, text-figs. 37, 38. (see also for earlier references).

Matonidium goepperti (Ett.) has been fully revised by Harris (1961) using abundant, well preserved material from the Yorkshire Jurassic. The English Wealden material is scanty and ill-preserved but agrees in all available characters with the Yorkshire material and I regard the two as specifically identical.

Family **DIPTERIDACEAE**

Genus ***HAUSMANNIA*** Dunker 1846 : 12

Hausmannia dichotoma Dunker

Pl. 3, figs. 1, 2

1846 *Hausmannia dichotoma* Dunker : 12, pl. 5, fig. 1; pl. 6, fig. 12.
1894 *Dictyophyllum Roemeri* Schenk; Seward : 140, text-figs. 16, 17.
1906 *Hausmannia dichotoma* Dunker; Richter : 18, pls. 3–6.
1913 *Hausmannia pelletieri* Seward : 89, pl. 14, figs. 1–3.
1961 *Hausmannia dichotoma* Dunker; Harris : 126, text-fig. 43.

This species is widespread in the Lower Cretaceous of Europe and less common in the Jurassic. It has been revised by Harris (1961) who gives an emended diagnosis based on Richter's material (Lower Cretaceous; Germany) and on Yorkshire Jurassic specimens. The leaves of *H. dichotoma*, both sterile and fertile, are quite well known but nothing is yet known of the sorus. The English Wealden material consists of a few imperfect sterile leaves which add nothing to our knowledge of the species. The best examples are figured in Pl. 3, figs. 1, 2.

Family **SCHIZAEACEAE**

Genus ***RUFFORDIA*** Seward 1894 : 75

Ruffordia goepperti (Dunker)

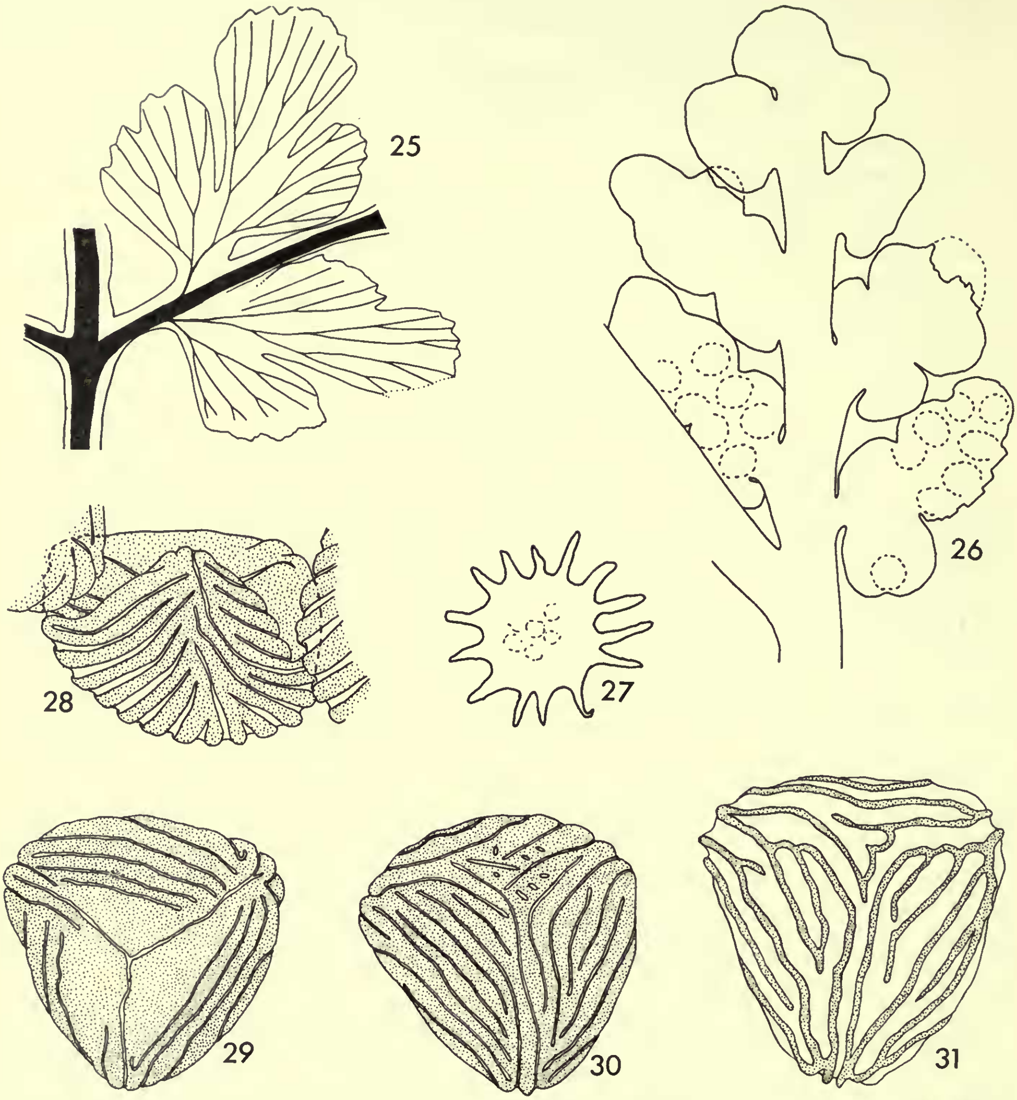
Pl. 4, figs. 1–7; Pl. 5, figs. 1–4; Text-figs. 25–31.

Selected references:

1843 *Cheilanthites Göpperti* Dunker : 6.
1894 *Ruffordia Göpperti* (Dunker) Seward : 76, pl. 3, figs. 5, 6; pl. 4; pl. 5, figs. 1–5.
1894 *Ruffordia Göpperti* (Dunker) var. *latifolia* Seward : 85, pl. 6, figs. 1, 1*a*.
1910 *Ruffordia Goepperti* (Dunker); Seward : 350, text-fig. 260 A–C. (figures repeated from Seward 1894).
1913 *Ruffordia goepperti* (Dunker); Seward : 91, text-fig. 2A. (drawing of a spore).
1921 *Ruffordia Goepperti* (Dunker); Halle : 10, pl. 2, figs. 1–8.
1958 *Ruffordia goepperti* (Dunker); Couper : 109, pl. 17, figs. 4–6. (photographs of spores).
1966 *Ruffordia goepperti* (Dunker); Hughes & Moody-Stuart : 274, pl. 43, figs. 1–12. (spores).

EMENDED DIAGNOSIS. Frond triangular, tripinnate to quadripinnate; rachis slender. Pinnae triangular or ovate; primary pinnae nearly opposite; secondary pinnae increasingly alternate. Sterile and fertile parts distinct. Sterile pinnules variable in width, decurrent; narrow pinnules linear, apices mucronate or acute, venation Coenopterid; wider pinnules ovate, Sphenopterid, with small marginal tooth at each vein ending. Fertile pinnules reduced in length but not breadth; more widely outspread, not decurrent, margins undulating, apices bluntly rounded. Sporangia borne singly on underside of pinnules without indusium; typically twelve on a pinnule, arranged in two longitudinal rows. Annulus transverse, apical,composed of about fifteen to twenty-five long narrow cells radiating from a central plate; extending at least to middle of sporangium. (Remaining parts of sporangium unknown, spore number uncertain). Spores rounded-triangular with convex sides, typically 45 μ equatorial diameter (range 35 μ to 60 μ), tri-radiate cracks almost reaching corners. Apical parts of facets smooth, rest of facets and whole of distal surface covered with ribs separated by grooves. Ribs forming three sets, each set starting on contact face and extending on to distal surface; in each set ridges nearly parallel. Ridges of a set joining near tri-radiate cracks and also joining, though less regularly, along continuation of tri-radiate cracks onto back of spore. Smooth apical parts of facets as thick as ribs.

DESCRIPTION AND DISCUSSION. *Ruffordia goepperti* (Dunker) is represented by a large number of sterile specimens which show a wide range in the form of the pinnules, the extremes of which are shown in Pl. 4, figs. 1, 4. The specimens with broadest pinnules were designated *R. goepperti var. latifolia* (Seward 1894) but all are now included in *R. goepperti* (Dunker) as there seems to be intergradation, though the possibility of the widest forms belonging to a different species is not excluded. There are three fertile specimens amongst the English material (V.2160 V.2295, V.2192). Two are completely fertile (V.2160 and V.2192) whilst the other (V.2295) has basal fertile pinnae and a sterile top (Pl. 5, fig. 1). Specimens V.2192 and V.2295 are preserved in the characteristic red ironstone and only the spore masses, and sometimes the sporangium annulus, are well preserved, the rest of the



FIGS. 25–31. *Ruffordia goepperti* (Dunker). 25. Broad form of pinnules showing venation. V.2357. × 8. 26. Fertile pinnules showing undulating margins. Broken lines indicate positions of sporangia. V.2160. × 15. 27. Sporangium showing thickened walls of annulus. V.2295. × 100. 28. Spore in equatorial view showing widely spaced ribs and shapes of ribs in section, i.e. rounded, flattened, grooved. Slide from V.2160, × 750. 29, 30. Proximal and distal surfaces of the same spore showing wide ribs closely spaced. Slide from V.2160, × 750. 31. Spore with narrow ribs and wide grooves. Slide from V.2192*b*, × 750.

frond being only a faint impression on the rock. This is a typical condition of the plants in this matrix but it is sometimes useful for details of venation (Pl. 4, fig. 7). Specimen V.2160 in a soft, fine, grey siltstone matrix is much better preserved though the frond is heavily varnished and badly cracked. Text-figure 26 shows the rounded lines of the fertile pinnules with a lobed appearance. The specimen presents the upper surface of the frond and the sporangia below are seen only in faint outline. A balsam transfer revealed no details of the sporangia.

The spores of *R. goepperti* (Dunker) were inadequately figured by Seward (1913, text-fig. 2A) using V.2192 and by Couper (1958, pl. 17, figs. 4–6) using Seward's slide preparation. Recently the spores have been studied in detail by Hughes & Moody-Stuart (1966) using V.2192 and Seward's slide mentioned above. I have found that V.2192 yields spores which are somewhat different from those of V.2295 and V.2160. The spores agree in size range and general form but differ in details of sculpturing. The spores from V.2295 and V.2160 have ribs (muri) from 2 μ to 5 μ wide separated by furrows (lumina) 0·5 μ to 2 μ wide but the ribs of any particular spore are always wider than the furrows and the majority of spores have ribs about 3 μ wide and furrows 1 μ wide (Text-figs. 28–30). The ribs vary in profile and may be rounded, flattened or indented; this variation is seen in Text-fig. 28. Spores from V.2192 have the sculpture in almost exactly the reverse proportions (Text-fig. 31), the ribs being 1 μ to 2 μ wide and spaced 2 μ to 5 μ apart. Hughes & Moody-Stuart (1966) give a detailed diagnosis of these spores and numerous figures. I have prepared spores from various parts of V.2192 but I have been unable to find any with broad ribs. Neither V.2295 nor V.2160 yielded spores with narrow ribs and I could find no suggestion of gradation between the two types of spores.

The identity of V.2192 is not in doubt, however, because in all other respects it agrees perfectly with the other two specimens. It is closely similar to the basal pinnae of V.2295 and also has undulating pinnules as in V.2160.

Fertile specimens of *R. goepperti* (Dunker) from Manchuria were figured by Halle (1921) including photographs of the sporangia, each represented by a well preserved annulus. This annulus is certainly an apical ring of the Schizaeaceous type. Halle's photographs show the long annulus cells radiating from a small circular space or " plate ". This suggests that the annulus cells in Text-fig. 27 do not show their full length, although he does report cases where the " central area seems to be much wider than others ". Halle removed what he considered to be a whole sporangium and gives three countings in the region of 400. I have removed what appeared to be whole sporangia from the balsam transfers and obtained various counts under 100. I regard my counts as highly suspect as it was difficult to be sure that the spore masses were whole sporangia. One cannot know how reliable Halle's count is but he reports that " in some cases it was possible to remove the whole contents of a sporangium more or less intact ". In living members of the Schizaeaceae the spore output is 128 or 256. Hughes & Moody-Stuart (1966) regard the spores of Halle's material as of a different type from those found in *R. goepperti* (Dunker) from the English Wealden. However, his photographs of sterile and fertile fronds appear to be very similar to the English specimens. One of them (pl. 2, fig. 2) shows short, undulating, fertile pinnules. Halle's photograph of the spores (pl. 2, fig. 8) is a poor one and considering the spore differences in the English specimens of *R. goepperti* (Dunker) I have retained the Manchurian material within the species until it can be proved otherwise. Certain details of the sporangium in the diagnosis above are based on Halle's account.

Among living genera of the Schizaeaceae, *R. goepperti* (Dunker) most resembles *Anemia* with its distinct and reduced fertile pinnae. The sterile frond of *Anemia adiantifolia* is very similar in form to the broader specimens of *R. goepperti* whilst the narrow pinnules closely resemble *Anemia cuneata* (Bower 1926, text-fig. 440).

The sculptured spores of the genus *Mohria* are of exactly the same type as *R. goepperti* (Dunker). This type of spore also occurs in the other Wealden Schizaeaceous fern, *Pelletieria valdensis* Seward and a comparison is included in the descrition of that species.

Genus ***PELLETIERIA*** Seward 1913 : 91

Pelletieria valdensis Seward

Pl. 6, figs. 1, 2; Text-figs. 32–40

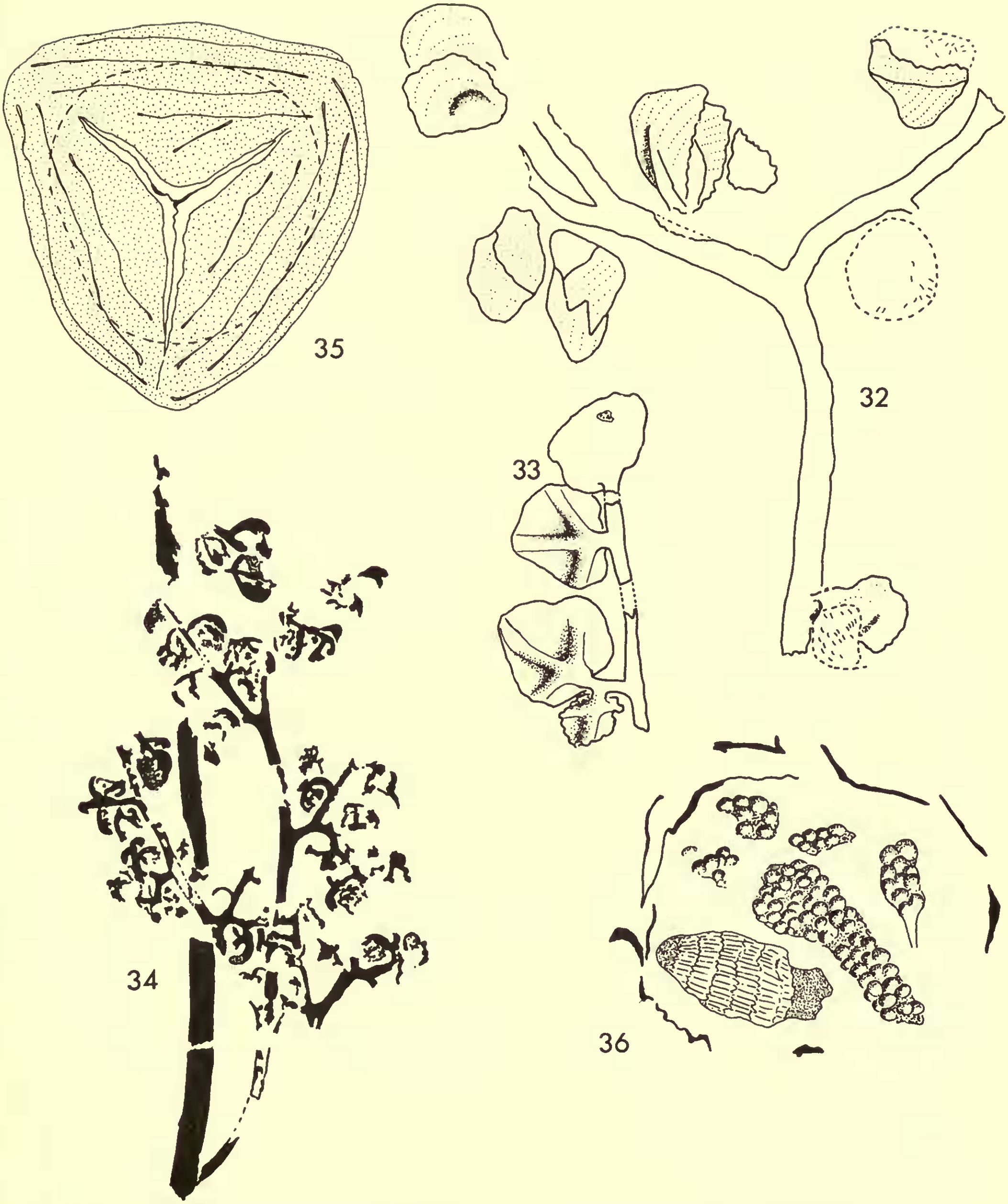
1913 *Pelletieria valdensis* Seward : 91, text-figs. 2B, 3, 4; pl. 12, figs. 12*a*, 12*b*; pl. 14, fig. 5.
1958 *Pelletieria valdensis* Seward; Couper : 109.
1966 *Pelletieria valdensis* Seward; Hughes & Moody-Stuart, pl. 44, figs. 1–8; pl. 45, figs. 1–7.

EMENDED DIAGNOSIS. Known only from fertile specimens. Frond at least quadripinnate; consisting of slender axis branched repeatedly, with no lamina except at tips of ultimate branches. Tips bearing groups of fertile pinnules; each pinnule tightly rolled, completely enclosing the sporangia. Each rolled pinnule more or less spherical, 2 mm. across, enclosing at least ten sporangia; sporangium elongated, sessile or shortly stalked, wall composed of small elongated cells, longitudinally orientated. (Annulus unknown). Spores rounded-triangular with tri-radiate cracks of medium length; surface sculptured with a pattern of flat ribs 3–7 μ wide separated by narrow grooves 0·5–2 μ wide.

LECTOTYPE. V.2329. Selected Hughes & Moody-Stuart 1966.

DESCRIPTION. *P. valdensis* Seward is represented by several specimens all of which are fertile. Fragments of pinnae and detached fertile " capsules " are abundant but there are only two assembled groups of pinnae, specimens V.2368 and V.2329. Both of these syntypes were figured by Seward (1913, text-figs. 3B, B'; pl. 12, figs. 12*a*, *b*.) and V.2329 (Text-fig. 32) has recently been selected as Lectotype by Hughes & Moody-Stuart (1966). After I picked away the matrix V.2368 is now a better specimen, more extensive and better preserved than V.2329 (Pl. 6, figs. 1, 2, Text-fig. 39).

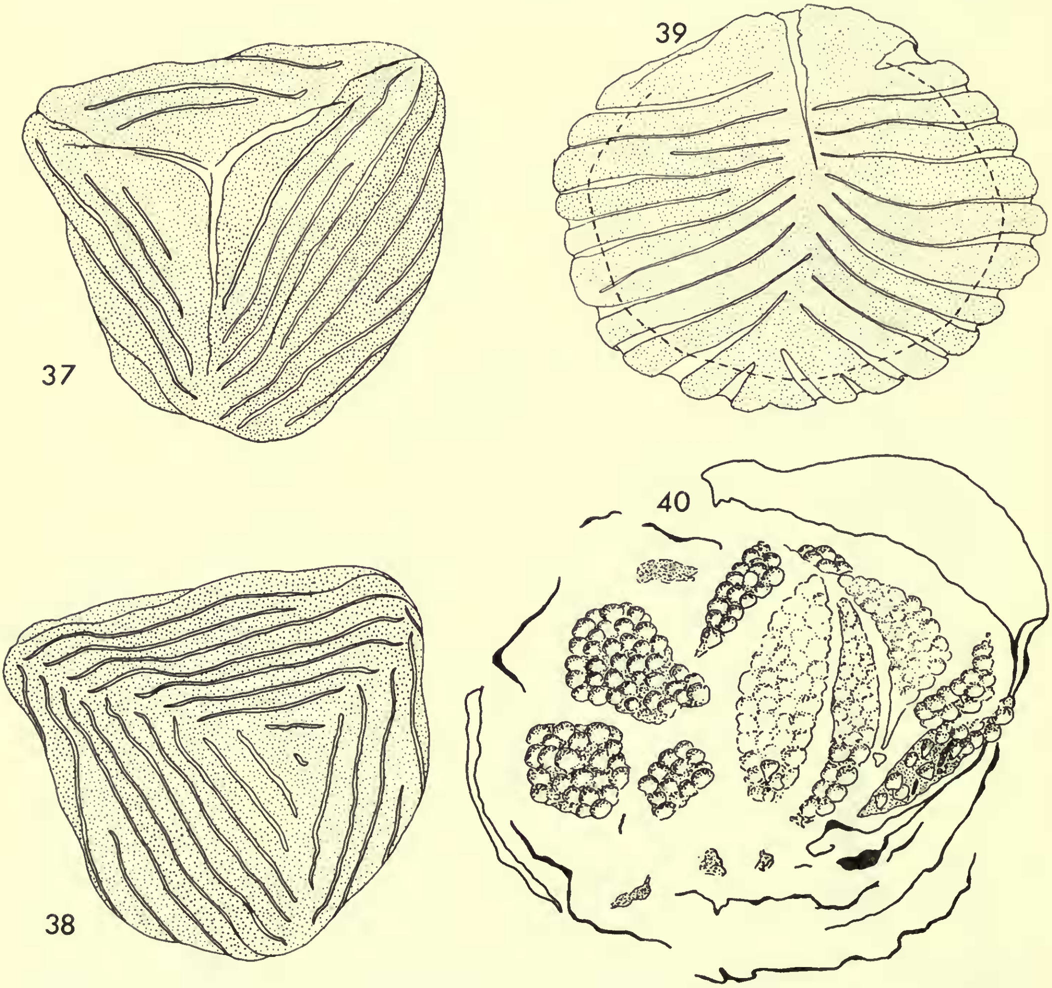
The exact form of the fertile " capsules " is far from fully understood. A number of isolated " capsules " were dissolved out of the rock in HF but revealed nothing more about their structure than is shown in the Lectotype which clearly shows the folded nature of the pinnules (Text-fig. 32). A number of specimens show hairs in the matrix where " capsules " have been removed (Text-fig. 32) but such hairs could



Figs. 32–36. *Pelletieria valdensis* Seward. 32. Lectotype showing folded " capsules ", hairs and cell directions (indicated by dotted lines). V.2329. × 6. 33. Small specimen with three ribs on the " capsules ". V.51846. × 6. 34. Largest assembled shoot showing dissected form of frond. V.2368. × 3. 35. Spore showing thickness of wall (indicated by dotted line) V.51841. × 750. 36. Eroded " capsule " with one sporangium showing cells of the wall. Others showing spores. V.51847. × 35.

not be found on any of the specimens dissolved out. Certain specimens show the axis continued as a rib over the back of the rolled fertile pinnules and this rib is branched in V.51846 (Text-fig. 33). The pinnules of V.51846 appear less tightly rolled than others and might well prove worth sacrificing to a balsam transfer. That this specimen is fertile is not in doubt as spores can be seen through a broken part at the top.

Because the sporangia are completely enclosed they could only be studied in certain eroded " capsules " which show sporangia in various attitudes (Text-fig. 40).



FIGS. 37–40. *Pelletieria valdensis* Seward. 37, 38. Proximal and distal surfaces of the same spore. Slide from V.2329, × 750. 39. Equatorial view of spore showing widely spaced ribs. Slide from V.51841, × 750. 40. Eroded " capsule " with folded pinnules in section and spores in sporangia. V.51840. × 35.

Attempts to isolate a sporangium failed because the plant material crumbles very easily into small fragments: thus the spore number is not known. However, on such a sporangium as in the centre of Text-figure 40 around fifty spores can be counted on the surface but because only one layer can be seen it seems probable that the contents are at least twice this figure. One sporangium seen in surface view (Text-fig. 36) shows the cells of the wall, small, elongated and longitudinally orientated; although there is no indication of the annulus.

The spores of *P. valdensis* Seward have recently been redescribed by Hughes & Moody-Stuart (1966) using Seward's figured slide preparation from V.2329 (1913) and new preparations from V.2329. They found the size range to be 52–98 μ with 80% of specimens between 63 μ and 84 μ maximum diameter. My preparations from V.2329 and V.21841 agree well with these figures but V.2368 yielded somewhat larger spores, 56–115 μ (100 measured) with 75% between 75 μ and 105 μ. Hughes & Moody-Stuart (1966) have diagnosed, described and figured the spores in detail and there is nothing more to add.

COMPARISON. The ribbed spores of *P. valdensis* Seward are typically Schizaeaceous and very similar to those of various living and fossil species. However, the form of the fertile fronds cannot be matched; the living members of the Schizaeaceae merely having curled margins protecting the sporangia. The only comparable structure I know is in the species *Onoclea sensibilis* Linn, where the fertile pinnules are narrow and so tightly inrolled as to completely enclose the sporangia.

The spores of *P. valdensis* are similar in form to those of *Ruffordia goepperti*, particularly the form with the broad ribs and narrow grooves, but they are quite easily distinguishable on size difference alone. The upper limit found for the diameter of *R. goepperti* was 60 μ and the lower limit for *P. valdensis* 63 μ. A most distinct difference is the thickness of the exine; in *R. goepperti* about 4 μ (including the thickness of the ribs) whilst in *P. valdensis* (Text-fig. 35) it varies from about 5 μ to 15 μ. This variation depends upon the spaces between ribs being open or closed and is dealt with in some detail by Hughes & Moody-Stuart (1966 : 280–282). A further difference is that the ribbed pattern in *P. valdensis* extends on to the contact facets whilst in *R. goepperti* the facets are smooth.

Family **POLYPODIACEAE**

Genus ***ASPIDISTES*** Harris, 1964 : 181

The type species of this genus, *Aspidistes thomasi* Harris, is the only other Mesozoic fern I know with the *indusium superum* and other aspidioid characters. Although various diagnostic characters of *Aspidistes* are not known for *Aspidistes sewardi* sp. nov. the form of its indusium and spores give it a good measure of agreement. The slight difference in spore number (*A. thomasi* has forty-eight)is not important. However, further details of the sorus and sporangium may well show it to be generically distinct. Various other genera exist whose names suggest close affinity with *Aspidium* or *Polystichum* but are based only on sterile specimens.

Aspidistes sewardi sp. nov.

Pl. 6, figs. 3, 4; Text-figs. 41–43

1894 *Weichselia mantelli* (Brongniart) Seward : 121.

DIAGNOSIS. (Based on single fertile pinna V.2173*a*). Pinnules arising from upper surface of rachis at an angle of 50–60°; pinnules 2 mm. long, 1·5 mm. broad, apex rounded; joined to each other at base by a narrow web; margin of pinnules and web rolled. Groups of three sori borne on under surface of each pinnule; two larger adjacent to the rachis. Each sorus with a thick peltate indusium covering about twelve sporangia arranged in a circle. Sporangium containing thirty-two spores (sporangial wall unknown). Spores trilete, smooth walled, thickened at corners; narrow bands of thickening flanking triradiate crack. Arms of triradiate crack nearly reaching corners, sometimes bifid at ends; diameter 60–75 μ.

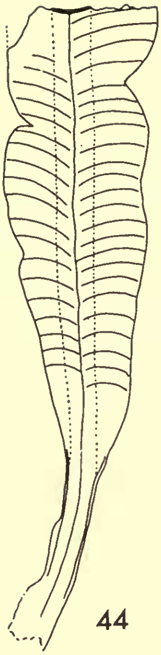
HOLOTYPE. V.2173*a*, the only specimen.

DESCRIPTION. The single specimen (V.2173*a*) is 6·5 cm. long and was formerly referred to *Weichselia mantelli* (= *W. reticulata* Stokes & Webb) by Seward (1894) its form being very similar to the smaller pinnules of that species. However its abaxial surface is uppermost and on moistening with paraffin the sori are clearly visible to the naked eye (Pl. 6, fig. 4). It is certainly not *Weichselia reticulata* for fertile material of that species is included in the Bommer Collection and it is quite different (correspondence with Dr. K. L. Alvin).

Unfortunately the specimen is heavily impregnated with glue and the substance of the fossil is badly crumbling, making it very difficult to examine the details of the sorus. The water soluble gum swells rather violently when wet and lifts the fossil fragments off the surface of the rock. Careful picking with a fine needle revealed a certain amount of information. The circular indusium appears to be quite thick and is probably attached by a central stalk; details of its cellular structure could not be seen. The sporangia are distinct pear-shaped masses, about twelve in number, in a ring under the indusium and sometimes a few under the rolled margin of the pinnule. They were easily removed intact to count the spores. Of the twelve sporangia macerated and counted nine contained thirty-two spores and three others contained twenty-nine, thirty, and thirty-one. The sporangial wall was not seen either in the untreated sporangium or during maceration.

Among the Wealden ferns there are few species of sterile fronds to which this specimen could belong but it is similar to one described as *Dichopteris delicatula* Seward (1913 pl. 11, figs. 6*a*, *b*). Possibly further specimens, sterile or fertile, are among the *Weichselia reticulata* material but nothing is known of its venation and it is not always clear in *Weichselia*. Furthermore any specimen with the adaxial side upwards would easily be missed.

COMPARISON. Amongst living genera *A. sewardi* is most similar to *Polystichum* agreeing in the form of the indusium and the spore output. However all living species of the Aspidieae have wedge-shaped spores whereas both *A. sewardi* and *A. thomasi* Harris have trilete spores.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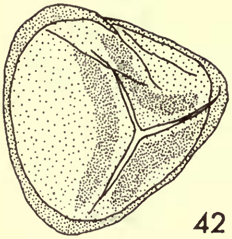
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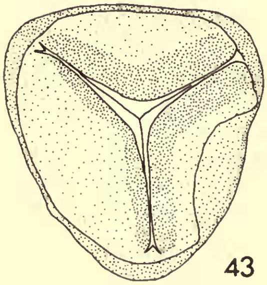
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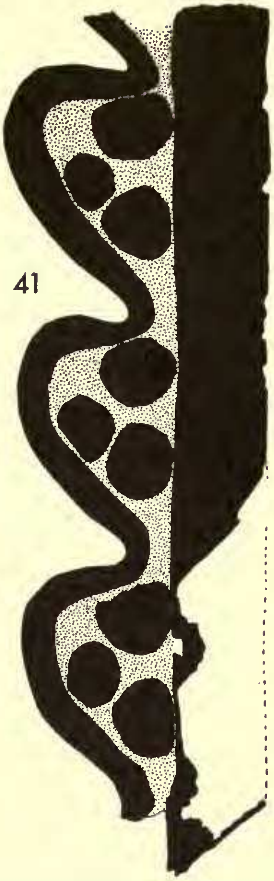
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FIGS. 41–43. *Aspidistes sewardi* sp. nov. 41. Three pinnules showing shape, rolled margins and sori. V.2173*a*, × 15. 42, 43. Two spores. Triradiate crack in Fig. 43 with bifid ends. Fig. 42, slide ii from V.2173*a*, × 750. Fig. 43, slide i from V.2173*a*, × 500.
FIG. 44. *Nilssonia schaumburgensis* Dunker. Base of leaf. Specimen L.5532 Manchester Museum, × 5.

A. sewardi is named after Sir Albert Charles Seward who first described the English Wealden flora.

UNCLASSIFIED FERNS

The following are ferns, described by Seward (1894), to which I can add little or nothing.

Cladophlebis longipennis Seward

1894 *Cladophlebis longipennis* Seward : 89, pl. 9, figs. 1, 1*a*.

Cladophlebis albertsii (Dunker)

1894 *Cladophlebis Albertsii* (Dunker) Seward : 91, text-fig. 9; pl. 8.

Cladophlebis browniana (Dunker)

1894 *Cladophlebis Browniana* (Dunker) Seward : 99, pl. 7, fig. 4.
1913 *Cladophlebis Browniana* (Dunker) Seward : 95, pl. 8, figs. 1, 2.

Cladophlebis dunkeri (Schimper)

1894 *Cladophlebis Dunkeri* (Schimper) Seward : 100, pl. 7, fig. 3.
1950 *Cladophlebis* (*Klukia*) *dunkeri* (Schimper); Radforth & Woods : 780, pl. 1.

The various English Wealden specimens, referred by Seward to the four species above, appear to be indistinguishable from each other and *Cladophlebis longipennis* Seward is particularly ill-defined. Indeed Seward himself later wrote (1913) of the " difficulty—or indeed, impossibility—of separating *Cladophlebis browniana* and *Cladophlebis dunkeri* ". Modern treatment of Canadian material referred to *C. dunkeri* (Schimper) by Radforth & Wood (1950) shows the fern to have Schizaeaceous sporangia and spores, though the latter are scarcely distinguishable in the photograph.

Sphenopteris ruffordi (Seward) comb. nov.

1894 *Acrostichopteris Ruffordi* Seward : 61, pl. 6, fig. 3.

Sphenopteris fittoni Seward

1894 *Sphenopteris Fittoni* Seward : 107, pl. 6, fig. 2; pl. 7, fig. 1.

Sphenopteris fontainei Seward

1894 *Sphenopteris Fontainei* Seward : 106, pl. 7, fig. 2.

Leckenbya valdensis (Seward)

1894 *Nathorstia valdensis* Seward : 145, pl. 7, fig. 5; pl. 9, figs. 2, 2*a*.
1894 *Leckenbya valdensis* (Seward) Seward : 384.
1895 *Leckenbya valdensis* (Seward); Seward : 225.
1911 *Gleichenites cycadina* (Schenk); Seward : 664.

Teilhardia valdensis Seward

1913 *Teilhardia valdensis* Seward : 96, pl. 11, figs. 7*a*–9*b*.

Genus ***ONYCHIOPSIS*** Yokoyama 1889 : 26

Onychiopsis psilotoides (Stokes & Webb)

1824 *Hymenopteris psilotoides* Stokes & Webb : 423, pl. 46, fig. 7.
1827 *Hymenopteris psilotoides* Stokes & Webb; Mantell : 55, pl. 1, figs. 3a, 3b; pl. 3, figs. 6, 7; pl. 3*, fig. 2.
1828*a* *Sphenopteris Mantelli* Brongniart : 50.
1828 *Sphenopteris Mantelli* Brongniart; Brongniart : 170, pl. 45, figs. 3–7.
1833 *Sphenopteris Mantelli* Brongniart; Mantell : 241.
1894 *Onychiopsis Mantelli* (Brongniart) Seward : 41, pl. 2, fig. 1; pl. 3, figs. 1–4.
1894 *Onychiopsis elongata* (Geyler); Seward : 55.
1905 *Onychiopsis psilotoides* (Stokes & Webb) Ward : 155, 506, 518, pl. 39, figs. 3–6; pl. 111, fig. 4; pl. 113, fig. 1.

1910 *Onychiopsis Mantelli* (Brongniart); Seward : 378, fig. 280, A, B.
1913 *Onychiopsis mantelli* (Brongniart); Seward : 96.
1961 *Onychiopsis psilotoides* (Stokes & Webb); Tattersall : 349, pl. 12, figs. 1–3.

DISCUSSION. This species was of world wide distribution in the Lower Cretaceous and its remains are known from England, Germany, France, Belgium, Portugal, Russia, Canada, U.S.A., Egypt, South Africa, India and Japan. Although the species has been described numerous times, including fertile parts (Tattersall 1961), it is still imperfectly known. Spores were readily obtained but resemble those of a number of families and do not help in classification. Details of sporangia are still unknown; though some fertile pinnules have a lumpy surface suggestive of sporangia. However the whole surface is covered by an indusium-like sheet of elongated cells and maceration leaves no trace of sporangial walls.

I have been unable to add usefully to our knowledge of this species and consider that the figures of Seward (1894) and Tattersall (1961) cannot be improved upon. In the light of a recent review of this species by Sukh Dev (1965) with an exhaustive synonymy I have given only those references which include the important name changes or refer to the English material.

Genus ***WEICHSELIA*** Stiehler

Weichselia reticulata (Stokes & Webb)

Pl. 6, fig. 5

Selected references:

1824 *Pecopteris reticulata* Stokes & Webb : 423, pl. 46, fig. 5; pl. 47, fig. 3.
1827 *Pecopteris reticulata* Stokes & Webb; Mantell : 56, pl. 3, fig. 5; pl. 3*, fig. 3.
1828*a* *Lonchopteris Mantelli* Brongniart; 60.
1828 *Lonchopteris Mantelli* Brongniart : 369, pl. 131, figs. 9, 10.
1894 *Weichselia Mantelli* (Brongniart) Seward : 114, text-figs. 12, 13.
1899 *Weichselia reticulata* (Stokes & Webb) Ward : 651, pl. 160, figs. 2–4.
1919 *Weichselia reticulata* (Stokes & Webb); Florin : 305, figs. 1, 2–5.
1965*a* *Weichselia reticulata* (Stokes & Webb); Reymanówna : 16, text-fig. 1; pl. 1, figs. 7–11.
1965 *Weichselia reticulata* (Stokes & Webb); Sukh Dev : 73, figs. 7, 8.

DISCUSSION. This widespread Lower Cretaceous species has recently been revised by Reymanówna (1965*a*) and Sukh Dev (1965). Most of the English specimens are mere fragments of pinnae, many of them fusainized, but there is one large, assembled frond in the collection. This is figured by Seward (1894, pl. 10, fig. 3.) and shows the characteristic habit of the plant very well.

The lower epidermis of *W. reticulata* (Stokes & Webb) was first figured by Florin (1919) using Belgian material and Sukh Dev (1965) has figured the epidermis from English Wealden specimens. Reymanówna (1965) gives figures of stomata together with photographs of indusia, but the fertile material of *W. reticulata* (Stokes & Webb) has yet to be fully described. None of the English material is fertile.

Sukh Dev (1965) gives extensive references to older work so that only selected references have been cited above.

SPERMATOPHYTA

PTERIDOSPERMAE

Genus *PACHYPTERIS* Brongniart

1828 *Pachypteris* Brongniart : 49 (Name only).
1829 *Pachypteris* Brongniart : 166.
1964 *Pachypteris* Brongniart; Harris : 121 (Emended diagnosis).

Pachypteris lanceolata Brongniart

Pl. 1, fig. 6; Text-figs. 45–47

1828 *Pachypteris lanceolata* Brongniart : 50 (Name only).
1829 *Pachypteris lanceolata* Brongniart : 167, pl. 45, fig. 1.
1895 *Dichopteris* sp. cf. *D. laevigata* (Phillips) Seward : 184, pl. 12, fig. 6.
1964 *Pachypteris lanceolata* Brongniart; Harris : 137, text-figs. 55–58.

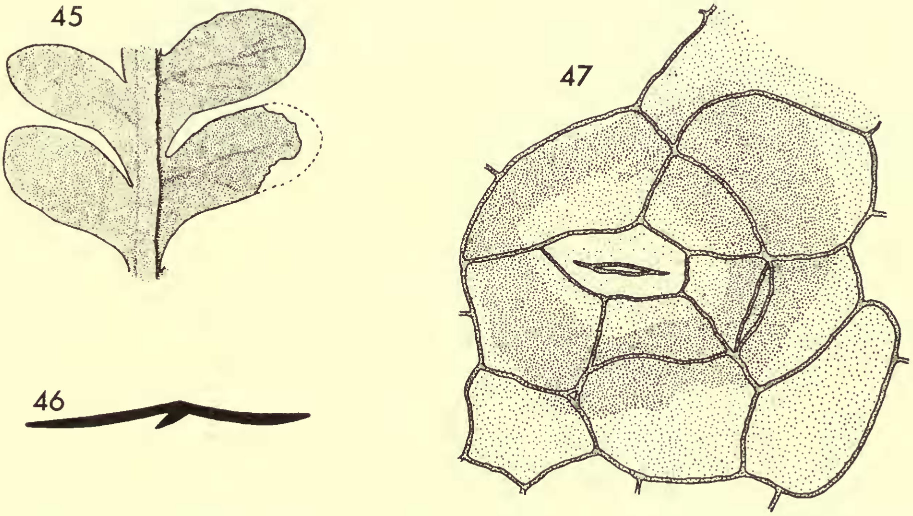
MATERIAL. V. 3245

DESCRIPTION. The following description is based on the only English Wealden specimen known. It is a single pinna, 8 cm. long, 1 cm. wide at the widest part, with two rows of pinnules, leathery in texture. The rachis, up to 700 μ wide, is very prominent on the underside of the pinna. The pinnules arise alternately, usually slightly overlapping but not completely divided and are up to 6 mm. long and 3 mm. wide, narrowing slightly but attached to the rachis by a broad and decurrent base. The pinnules are typically oval and blunt ended. Pinnules at the apex are smaller and less divided; the rachis is not so prominent here. The venation is visible on the lower side of some pinnules projecting slightly above the surface, but concealed in most, the veins consisting of a midrib with a few laterals given off at a fairly low angle. The midrib is broad and situated above the middle of the pinnule where it joins the rachis. The margins of the pinnules are not thickened.

The upper epidermis lacks stomata and has a thick cuticle showing isodiametric cells with smooth walls and without pits. These cells are irregularly arranged except at the margin where they are elongated and tend to be in longitudinal rows, the cells here having thicker anticlinal walls. The lower cuticle is thinner, the cells of the lower epidermis being thin walled, isodiametric and irregularly arranged, except at the margin and in the midrib region. The position of the midrib is indicated by a region of elongated, thicker walled cells in longitudinal rows. The margin is like that of the upper epidermis. Stomata are numerous on the lower side but absent from the midrib and marginal regions. They are slightly sunken, irregularly orientated and distributed and are almost always separated by ordinary epidermal cells. The guard cells are thinly cutinized except along the edges of the stomatal aperture where there is a thicker rim; the aperture is elongated. Subsidiary cells, usually six in number, form a ring and are generally smaller than the other epidermal cells. They have thicker cuticle on the periclinal walls which forms a ring round the stoma but are not thus thickened adjacent to the stomatal pit. Encircling cells are occasional and unspecialized. Trichomes are absent.

DISCUSSION. The preservation is good though the surface is somewhat cracked and because of the shortage of material available only a little could be macerated.

However, it was established that the specimen is attached to the rock by its upper surface and that whilst the lower cuticle is complete most of the upper is missing, only a narrow strip remaining around the edge of the pinnules. Thus very little upper cuticle has been examined and it is not known whether it had any stomata nearer the middle of the pinnule. Only a few of the pinnules show the positions of the midrib and the laterals on the underside, and at best they are indistinct. An attempt was made to see the venation by transmitted light during maceration but this failed. The prepared cuticle, whilst showing the position of the midrib by the elongated cells and lack of stomata, gives no indication of the position of the lateral veins.



Figs. 45–47. *Pachypteris lanceolata* Brongniart. 45. Part of pinna showing venation. V.3145. × 4. 46. Reconstructed transverse section of pinna showing prominent rachis on lower side. ×4. 47. A single stoma. The darker stippling indicates the ring of thicker cuticle. Slide V.3145*b*. × 700.

The surface of the specimen viewed in reflected light shows very clearly the cells of the lower epidermis with a divergent trend in relation to veins. In the fragmentary cuticle preparations this trend is not apparent and the cells appear haphazard in arrangement. One very prominent cell was seen, the nature of which is obscure though it is certainly not stomatal. It is possibly a trichome base though no similar cells could be identified with certainty.

Comparison. A careful comparison was made with specimens of *Pachypteris lanceolata* Brongn. from the Yorkshire Jurassic (Harris 1964). The Yorkshire material is known in much more detail, numerous specimens being available some of which are complete leaves. A notable feature of *P. lanceolata* is its wide range in form with intergradation between the extreme types. These include forms with small oval pinnules, others with small narrow pinnules and much larger forms with lanceolate pinnules. Forms just like the present specimen occur. The cuticles of the various forms although basically the same show a certain variety in details such as number and size of stomata. Some have a large number of stomata close together while in others they are more widely spaced. The cuticle of the present fossil shows more widely spaced stomata than most of the specimens attributed by Harris to *P. lanceolata* but some of the latter approach the Wealden form very closely. These include specimens from Boulby Alum Quarry, Shale 2B; Whorlton, Scugdale, Rank Crag Soft Jet and Eston Moor, Beacon Quarry. It should be pointed out that these are not ordinary specimens but merely cuticle fragments obtained by maceration and identified on their microscopic characters.

As in the Wealden fossil, the stomata of the Jurassic *P. lanceolata* avoid the midrib and margins and are indistinguishable in structure. There is also very close similarity in size and shape of the ordinary epidermal cells, indeed some of the cuticle fragments of the two fossils could scarcely be told apart.

What little is known of the venation of the Wealden form simply affords more evidence of the similarity between these two fossils and consequently I have placed the Wealden specimen in the same species.

GYMNOSPERMAE

CYCADALES

Genus *NILSSONIA* Brongniart

Nilssonia schaumburgensis (Dunker)

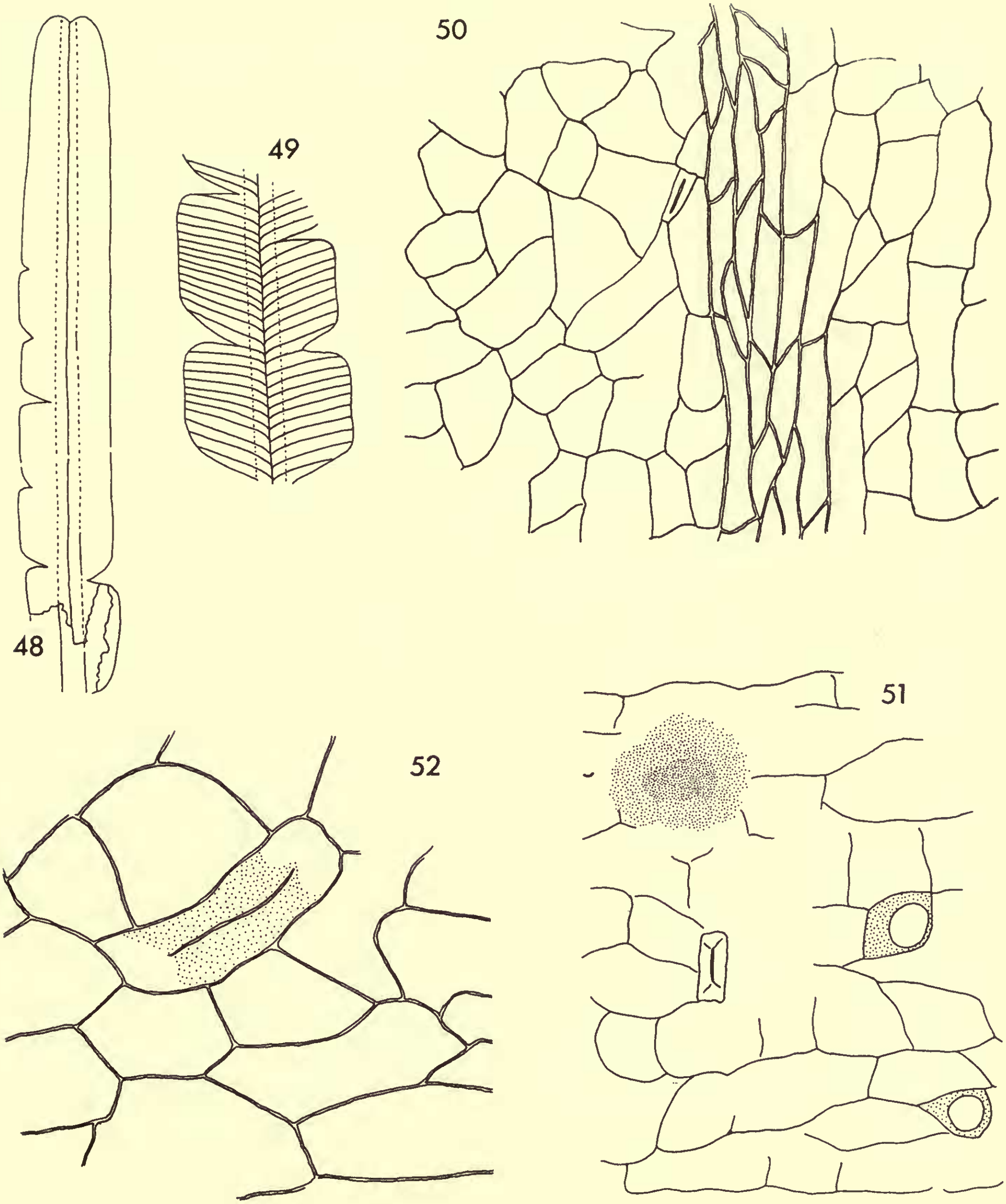
Text-figs. 44, 48–52

Selected references:

1846 *Pterophyllum schaumburgense* Dunker : 15, pl. 1, fig. 7; pl. 2, fig. 1; pl. 6, figs. 5–10.
1871 *Anomozamites schaumburgense* (Dunker) Schenk : 231, pl. 33, figs. 1–9.
1890 *Nilssonia cf. schaumburgensis* (Dunker) Nathorst : 5, 9, 13, pl. 1, figs. 6–9*a*.
1895 *Nilssonia schaumburgensis* (Dunker); Seward : 53, text-fig. 3.
1905 *Nilssonia schaumburgensis* (Dunker); Fontaine *in* Ward : 303, pl. 72, figs. 17–21.

EMENDED DIAGNOSIS. Leaf linear; width usually 3–5 mm., rarely up to 12 mm.; length unknown but at least 9 cm. Apex rounded and notched; base tapering. Midrib 1–2 mm. wide, depressed on upper surface, depression not narrowing towards apex. Lamina entire or more or less divided. Surface of lamina flat or slightly convex upwards. Veins fairly prominent, projecting above and below; arising from midrib at an angle between 70° and 80°; concentration of veins typically three to four per mm.

Cuticle of moderate thickness but anticlinal walls often obscure. Marginal cells of leaf and pinnae elongated parallel to edges and having thicker and more distinct anticlinal walls. Cells in main part of lamina tending to be elongated almost at right angles to edge, parallel with veins. Upper cuticle without stomata or trichomes, positions of veins scarcely distinguishable. Lower cuticle not showing positions of veins clearly but cells with slight tendency to be more elongated over veins. Stomata scattered between veins; small, inconspicuous and scarcely sunken.



FIGS. 48–52. *Nilssonia schaumburgensis* (Dunker). 48. Leaf, slightly divided, showing form of apex. Position of rachis indicated by dotted line or solid line where lamina is broken and rachis is exposed. V.3762. × 2. 49. More divided leaf showing the veins. Position of rachis shown by dotted lines. V.2171. × 5. 50. Cuticle showing elongated cells of leaf edge in centre, lower surface to the left, upper surface to the right. Slide from V.1436. × 300. 51. Lower cuticle showing a resin body, a stoma and two single-celled trichome bases. Slide from V.2171**. × 300. 52. Single stoma showing exposed guard cells. Slide from V.3762. × 700.

Guard cells exposed; 30–50 μ long and about 15 μ wide, surrounded by several unspecialized and ill-defined subsidiary cells. Unicellular trichome bases scattered over whole lower surface; thickly cutinized except for central circle. Resin bodies occasionally seen, about 50 μ across. Reproductive organs unknown.

DESCRIPTION. This small *Nilssonia* is represented by more than a dozen specimens from the English Wealden. They show a good deal of variety in the form of the lamina, some being entire, others slightly and irregularly divided, others regularly and completely divided almost to the midrib. Only two specimens are more than 6 mm. wide, V.2171*a* which is 12 mm. wide (Seward 1895 : 53, text-fig. 3*c*) and V.3731 which Seward labelled as *Taeniopteris beyrichii* var *superba*. Both agree with the others in their cuticle. All but one specimen have the adaxial surface exposed and in these the midrib is seen only when the substance of the lamina is broken away (Text-fig. 48) but in all specimens its position is indicated by a depression of the lamina. This depression retains its width to the apex of the leaf. V.3731 is the only specimen with the lower surface uppermost and is the largest specimen, 9 cm. long (incomplete) and 11 mm. wide, tapering to 4 mm. near the base. The rachis is 2·5 mm. wide whilst in most specimens it is little more than 1 mm.

Resin bodies are rare; they are not seen on the surface of the fossils and only three were seen in macerated cuticle fragments.

The stomata are particularly difficult to distinguish and were identified with certainty on only a very few pieces of lower cuticle. The stoma in Text-fig. 52 is the best example seen and shows a slight surface thickening in the middle region of the guard cells.

DISCUSSION. *Nilssonia schaumburgensis* has been identified by numerous authors from several countries. In all cases there is very little detail on which to compare the various accounts. From the few details available, i.e. size, shape and vein concentration the English material agrees well with the type-material described by Dunker (1846) and the specimens figured by Schenk (1871), Nathorst (1890) and Fontaine *in* Ward (1905).

COMPARISON. *N. revoluta* Harris (1964) from the Jurassic (Upper Deltaic) of Yorkshire is the only other species I know which is as small as *N. schaumburgensis*. The leaves are similar in size and are entire; also the vein concentration is similar, up to thirty per cm. Another similarity is that the veins are scarcely shown in the upper cuticle, however they are strongly indicated in the lower cuticle. Rather different characters shown by *N. revoluta* include conspicuous cell outlines with nodular thickenings and bulging subsidiary cells.

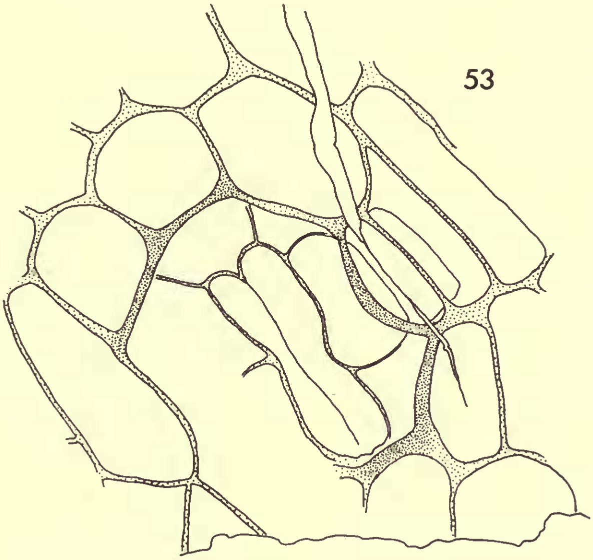
Genus **BECKLESIA** Seward 1895 : 179

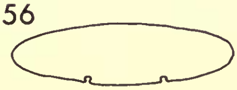
Becklesia anomala Seward

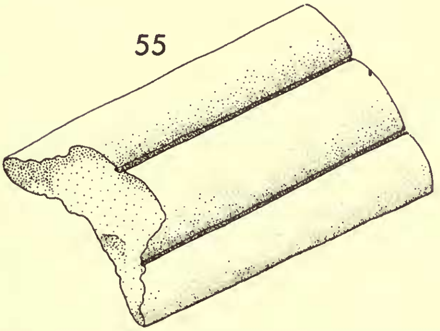
Text-figs. 53–56

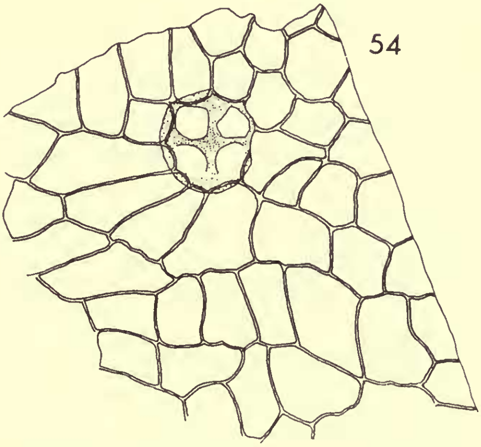
1895 *Becklesia anomala* Seward : 179, pl. 14, figs. 2, 3.

EMENDED DIAGNOSIS. Leaf simply pinnate, probably much longer than broad (whole leaf unknown), consisting of a slender rachis bearing two lateral rows of long straight pinnae. Rachis 6 mm. wide, pinnae arising at intervals of approximately 1 cm., at an angle of about 40°. Pinnae at least up to 10 cm. long, 3 mm. wide, narrowing to about 2 mm. near rachis (apex unknown), rounded in transverse section; margins of pinnae straight. Lower side of pinna having broad, flat midrib









FIGS. 53–56. *Becklesia anomala* Seward. 53. A single stoma. One hypodermal cell is seen on the right indicated by a single line; Slide from V.2361*a*. × 700. 54. A piece of cuticle from a non-stomatal region of the leaf, showing a four-celled trichome base. Slide from V.2361*a*. × 200. 55. An unsquashed portion of the pinna showing the two narrow stomatal grooves on the lower side. V.2361*a*. × 10. 56. A reconstructed section of a pinna. × 10.

flanked by two very narrow, shallow stomatal grooves with lateral non-stomatal regions about as broad as the midrib; upper surface flat but some pinnae showing numerous raised trichome bases.

Cuticle about 2 μ thick in non-stomatal regions, very delicate in stomatal grooves. Ordinary epidermal cells of upper and lower surface large, thin walled and arranged in longitudinal rows; very varied in shape, either square, rectangular or quite irregular; typically 50 μ broad. Cells over midrib and at edges of pinna tending towards diamond shape. Anticlinal walls cutinized, usually straight but sometimes slightly sinuous. Presence of a hypodermis occasionally indicated, particularly near trichome bases. Trichome bases mostly occurring on upper surface but sometimes also in non-stomatal regions of lower surface; roughly circular in surface view, about 60–70 μ diameter, composed of up to four small, thick-walled cells tending to overlap other epidermal cells. Trichome bases not present on all pinnae. Stomata longitudinally orientated and scattered in grooves about 45 μ wide. Guard cells thinly cutinized, about 45 μ long with six to seven subsidiary cells surrounding and slightly overlapping them; guard cells and subsidiary cells slightly sunken in shallow stomatal pit, surrounded by thicker walled cells, inner walls of which form thickly cutinized pit rim. Ordinary epidermal cells between stomata much smaller than those in non-stomatal regions.

HOLOTYPE. V.2361*a*.

DESCRIPTION. This species is described from two specimens both of which are incomplete leaves with no complete pinnae. Whilst most of the pinnae have been squashed during preservation, two fragments are so preserved that they retain their original shape and thickness. One is about 1 mm. thick and shows particularly well that the stomatal grooves are shallow, that the midrib is flat, and that the margin is rounded in section.

Much of the plant substance is missing from the two specimens and what remains is very cracked, so that all cuticle preparations are small pieces. Cuticle from the non-stomatal regions was easily obtained but it was only with considerable difficulty that preparations of the stomatal grooves were made. All grooves are filled with matrix and have extremely delicate cuticle which disintegrates even when most carefully macerated. The stoma shown in Text-fig. 53 is from the best preparation obtained in which, unfortunately, all the stomatal pits contain debris which obscures some of the details.

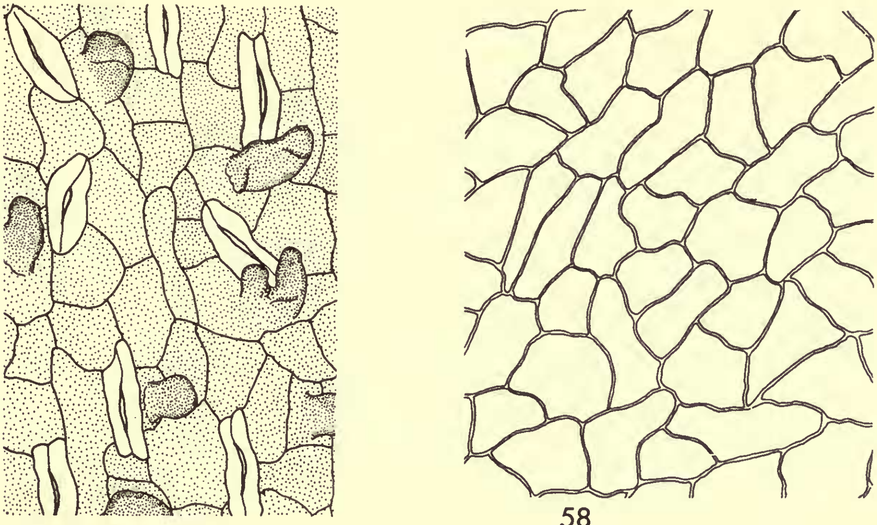
DISCUSSION. While the characters of this species are distinctly Cycadalean it is not closely comparable to any other genus, living or fossil. It is thus convenient to retain the original generic name. The stomatal grooves are much narrower than in any other Cycad. In *Cycas* stomata are present over the whole of the lower surface except the midrib and margins. The trichome bases of *B. anomala* are similar to those in *Cycas revoluta* (Pant & Mehra 1962, text-fig. 33D) but in that species they are two-celled.

Amongst fossil Cycads *Paracycas cteis* Harris (1964) from the Jurassic (Lower Deltaic) of Yorkshire is similar in size but differs in such features as wider stomatal bands and irregularly arranged stomata.

Becklesia sulcata sp. nov.

Pl. 2, fig. 6; Text-figs. 57–58

DIAGNOSIS. Pinnae up to 2 mm. wide (length unknown), with two narrow longitudinal grooves on lower side; stomata confined to these grooves. Grooves so placed that the central non-stomatal region is twice as wide as lateral non-stomatal regions. Margins smooth and entire. Cuticle moderately thick but much thinner in stomatal grooves. Non-stomatal region between grooves composed of cells in longitudinal rows, transverse anticlinal walls usually oblique, sometimes slightly sinuous. Cells of other non-stomatal regions not arranged in rows, very varied in shape and irregular in arrangement; walls often slightly sinuous. Guard cells extremely thinly cutinized, except for slight thickening around stomatal aperture. Guard cells about 50 μ long, not at all sunken, irregularly orientated but majority more or less longitudinal. Subsidiary cells very variable, not distinguished from other ordinary epidermal cells in groove, all of which are irregular in shape and size, smaller than epidermal cells of non-stomatal regions. Subsidiary cells often shared by adjacent stomata. Some of these cells bearing large, hollow, globular or elongated papillae; usually one such papilla near each stoma.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FIGS. 57, 58. *Becklesia sulcata* sp. nov. 57. Cuticle from a stomatal groove showing stomata and papillae. Holotype, V.51524. × 300. 58. Cuticle of upper side. V.51524. × 300.

HOLOTYPE. V.51524.

DESCRIPTION. This species is known only from cuticle fragments which are assumed to be pieces of pinnae although there is no direct evidence that they are from a pinnate leaf. However, it is so similar to *Becklesia anomala* Seward that I have placed it in the same genus. The main similarities are in such features as width of pinnae, position and width of stomatal grooves and form of ordinary epidermal cells.

COMPARISON. *Becklesia sulcata* lacks the multicellular trichome bases of *B. anomala*, has thinner more exposed guard cells and has large papillae.

If the form of ordinary epidermal cells is any criterion in considering the affinities of these little known plants, these irregular yet characteristic cells are almost exactly the same as in many living Cycads e.g. *Cycas revoluta.*

GINKGOALES

Genus ***PSEUDOTORELLIA*** Florin 1933 : 142

EMENDED DIAGNOSIS. Leaves entire, linear to elliptic; apex rounded, narrowing at base. Two or more longitudinal veins formed by dichotomies chiefly in basal part, ending blindly. Stomata confined to lower side, always longitudinally orientated; haplocheilic, monocyclic or incompletely amphicyclic; guard cells sunken, strongly cutinized. Subsidiary cells four or more. Epidermal cells with straight or faintly sinuous outlines.

The new fossil described here is at least the ninth species of this genus to be described and it now seems necessary to emend the generic diagnosis as the original diagnosis is too narrowly defined for present purposes, based as it was on the single species *P. nordenskioldi* Florin. The simplified, broader diagnosis above will better serve to admit such a fossil as the new English Wealden species with its wide range of leaf form and scattered stomata.

TYPE SPECIES. *Pseudotorellia nordenskioldi* Florin 1933.

Pseudotorellia heterophylla sp. nov.

Pl. 6, figs. 6, 7; Text-figs. 59–64.

DIAGNOSIS. Leaves entire, showing wide range of size and shape from narrow and needle-like to broad and elliptic. Dimensions of holotype 12 mm. long and 3 mm. wide; longest leaf known 3 cm. long and 1 mm. wide; other leaves ranging between these two. Apex unknown. Petiole unknown.

Veins varying in number from two in narrowest leaf to eight in broadest, formed by dichotomies near base of leaf. Veins may converge near apex but end blindly. Interstitial ducts sometimes present between veins.

Cuticle thick and leathery. Stomata present on one side of leaf only, scattered over whole surface (presumably lower), not avoiding veins; longitudinally orientated, typically 80 μ long. Ordinary epidermal cells elongated, arranged in longitudinal rows, sometimes with elongated, thickened ridge along surface. Surface of cuticle frequently sculptured.

Guard cells sunken beneath subsidiary cells, strongly thickened at common junction wall with overlying subsidiary cells. Subsidiary cells six, usually papillose, papillae projecting over stomatal aperture. Stomata usually not upsetting sequence of cell rows, subsidiary cells continuous in their lines of ordinary epidermal cells. Sometimes small subsidiary cells coinciding with outer edge of guard cells, forming ring or partial ring of more specialized subsidiary cells. Encircling cells rare. Guard cells sometimes having long polar appendages.

Upper epidermis without stomata, composed of longitudinal rows of elongated cells with fairly thick walls, sometimes in " packets ", often having finely sculptured cuticle. Positions of veins not indicated on upper surface. Edges of leaf smooth with fairly thick rim of cuticle. Cuticle of all forms of leaf closely agreeing; only minor differences in size of stomata, degree of thickening and form of polar appendages of guard cells.

HOLOTYPE. V.51525.

DESCRIPTION. A considerable number of whole and broken leaves were obtained by bulk maceration of the same coaly material which yielded *Becklesia sulcata*. Besides these a few of the larger needles were picked off specimen V.2222 in the British Museum (Natural History) collections. Several fragments were also identified in washings from the core of a borehole drilled near Winchester. Most of the linear leaves were found only in short lengths whilst the large elliptical leaves were almost whole. However, on none of these is an apex or petiole present. The petiole presumably had one vein which dichotomized at the base of the leaf to give the two main veins which may further give off branches on their inner sides in the lower part of the leaf. The veins are then parallel along the length of the leaf but may converge slightly near the apex (Text-figs. 61, 62.) although they all appear to end blindly. The interstitial ducts which are often present between veins are of unknown nature but are possibly resin ducts or even subsidiary veins.

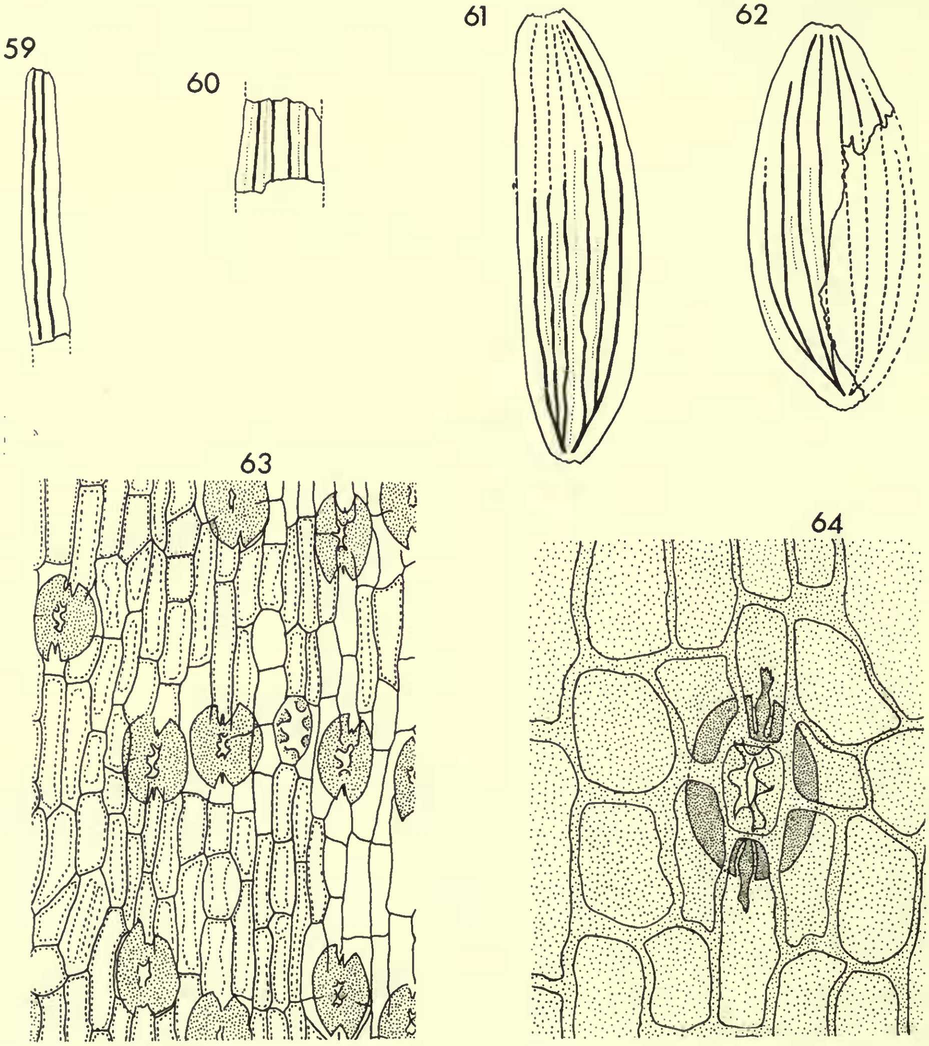
A number of leaves have what appear to be abortive stomata. One of these is seen in Text-fig. 63. No guard cells are developed but a ring of papillae surround the " guard cell mother-cell ". A few other " freak " stomata were seen where the guard cells were misplaced under the stomatal pit. Only one transversely orientated stoma was seen.

The differences in polar appendages of guard cells may be compared in Text-figs. 63, 64. Text-fig. 64 shows a stoma with the longest and most complex appendages projecting well beyond the ends of the guard cells. In Text-fig. 63 the appendages are quite short and pointed or scarcely developed at all. Also shown in Text-fig. 63 are some stomata with the subsidiary cells following the line of the guard cells as mentioned in the diagnosis.

COMPARISON. *P. heterophylla* shows a much wider range of leaf form than other species. *P. nordenskioldi* (Nathorst) described by Florin (1933), *P. minuta* (Nathorst) by Lundblad (1957), *P. ensiformis* (Heer) and *P. crassifolia* (Prynada) by Doludenko (Vachrameev & Doludenko 1961) all have the greatest width of their leaf situated towards the apex. *P. grojecensis* Reymanówna (1963), *P. ephela* (Harris 1935) and the elliptic leaves of *P. heterophylla* have the greatest width of the leaf situated in the middle region. *P. angustifolia* Doludenko and *P. longifolia* Doludenko

(Vachrameev & Doludenko 1961) both have long linear leaves of similar dimensions to some forms of *P. heterophylla*.

A common feature of the *Pseudotorellia* cuticle is the presence of median ridges of cuticle on the epidermal cells. *P. heterophylla*, *P. nordenskioldi*, *P. minuta*, *P. ephela* and *P. ensiformis* all have these ridges. In all, the epidermal cells are similar in form, longitudinally elongated. The packets of cells seen in the upper epidermis



Figs. 59–64. *Pseudotorellia heterophylla* sp. nov. 59–62. Various forms of leaf showing veins. Figs. 60–62 showing interstitial ducts. Fig. 59, V.51526, Fig. 60, V.51527, Fig. 61, Holotype, V.51525, Fig. 62, V.51528. All × 10. 63. Cuticle showing stomata, abortive stoma and ridges on the epidermal cells. V.51529. × 150. 64. Stoma with long polar appendages. Slide from V.2222. × 300.

of *P. heterophylla* (Pl. 6, fig. 6) are surpassed in development by those seen in *P. grojecensis*. In that species the packets consist of up to five cells and form a conspicuous pattern at right angles to each other (Reymanówna 1963, text-fig. 8A.)

The stomata of *P. heterophylla* appear to be more heavily cutinized than in other species. For instance in *P. ephela* and *P. grojecensis* the guard cells are heavily cutinized at the outer edges and along the stomatal aperture but in *P. heterophylla* the whole upper surface of the guard cells is heavily cutinized, but sometimes slightly thinner around the aperture.

The polar appendages of *P. heterophylla* are unique among the species under consideration for the rest have thin polar areas.

Papillate subsidiary cells like those in *P. heterophylla* are also present in *P. ephela*, *P. minuta* and *P. ensiformis* while *P. grojecensis* has a cuticular diaphragm on the surface of the guard cells around the aperture.

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EXPLANATION OF PLATES

Most of the figured specimen, are in the British Museum (Natural History) and bear the prefix V.

PLATE 1

Circonitella knowltoni (Seward)

FIGS. 1, 2. Gyrogonites showing five spiral cells meeting at the apical pole. Fig. 1, V.51552, Fig. 2, specimen lost. × 80.

FIG. 3. Basal pole of gyrogonite showing circular basal plate. V.51553. × 80.

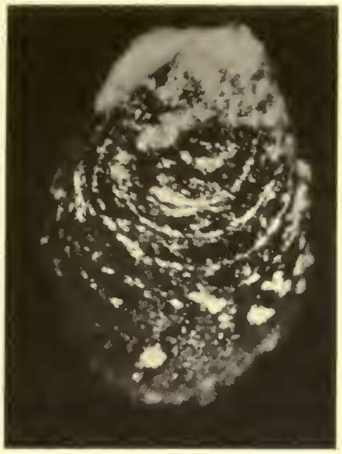
FIG. 4. Pyritised, unsquashed gyrogonite with convex spiral cells, showing basal plate. V.51554. × 80.

FIG. 5. Neotype with convex spiral partly broken away. V.51555. × 80.

FIGS. 1–5, individual specimens all from one block numbered V.51548 (re-registered from V.1070*a*).

Pachypteris lanceolata Brongniart

FIG. 6. Apical part of pinna, lower side uppermost, showing prominent midrib. V.3245. × 2.



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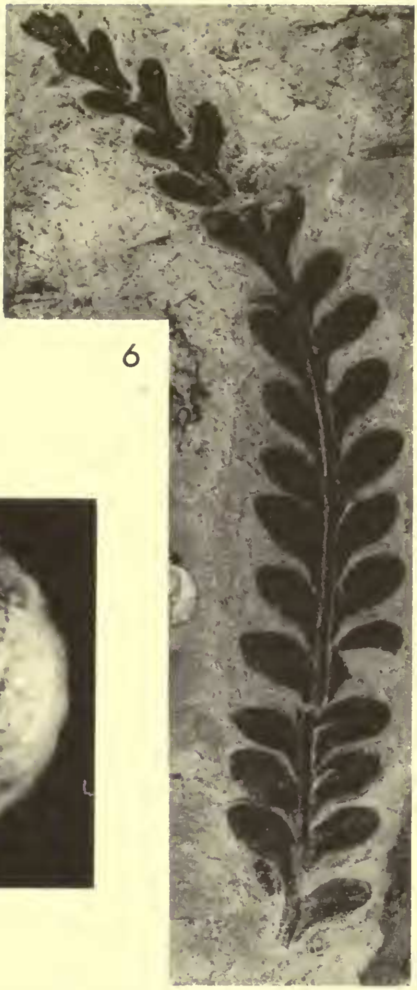

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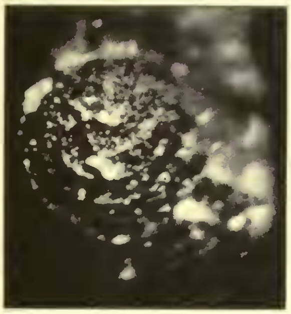

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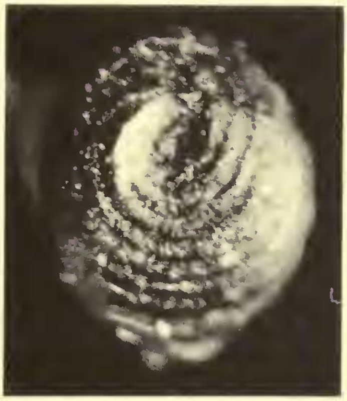

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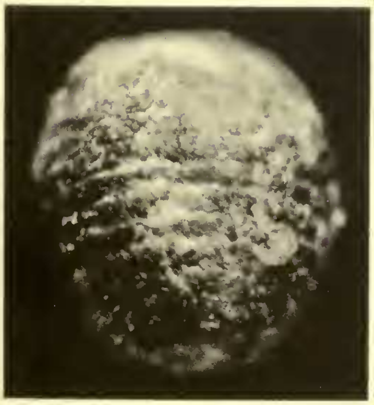

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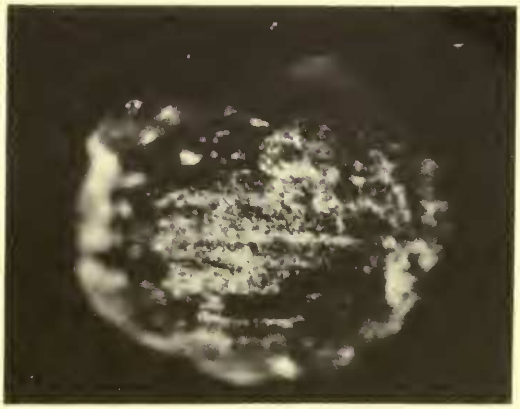


PLATE 2

Hepaticites zeilleri (Seward)

FIG. 1. General form of thallus showing dichotomous branching. Holotype, V.2330*a* × 1.

FIG. 2. Thallus showing thick midrib region and delicate lamina also rhizoids including detached bunches. V.2330*a*. × 3.

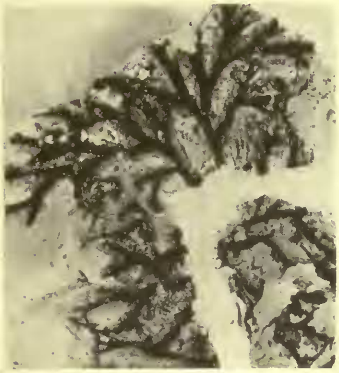
FIG. 3. Enlargement showing rhizoids pointing forwards between a dichotomy of the thallus. V.2330*a*. × 10.

Hepaticites ruffordi sp. nov.

FIGS. 4, 5. Thallus showing arcuate grooves, Fig. 4 immersed in paraffin, Fig. 5 coated with ammonium chloride. Holotype, V.2343. × 3.

Becklesia sulcata sp. nov

FIG. 6. Part of a pinna showing stomatal grooves. V.51540. × 20.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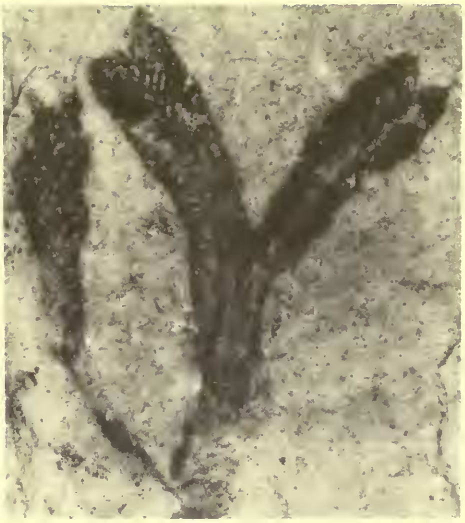
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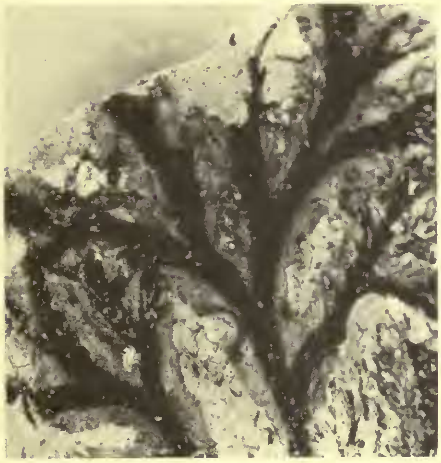
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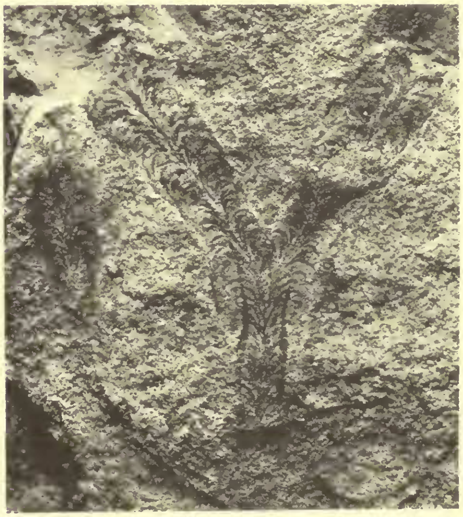
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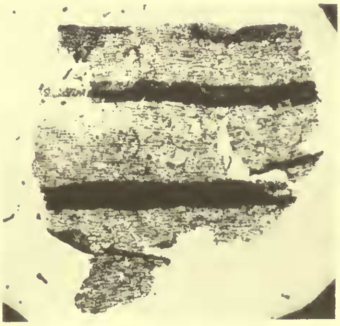
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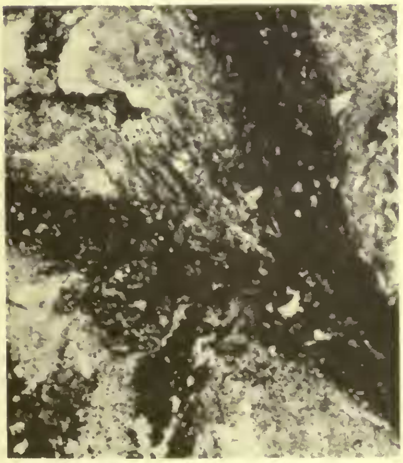
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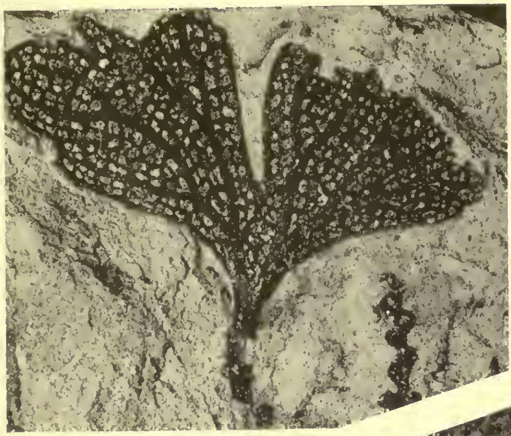
PLATE 3

Hausmannia dichotoma Dunker

FIG. 1. Small fan-shaped leaf with broken apices. Sterile. V.12317. × 3.
FIG. 2. Larger more divided leaf with strap-shaped segments. Sterile. V.12349. × 3.



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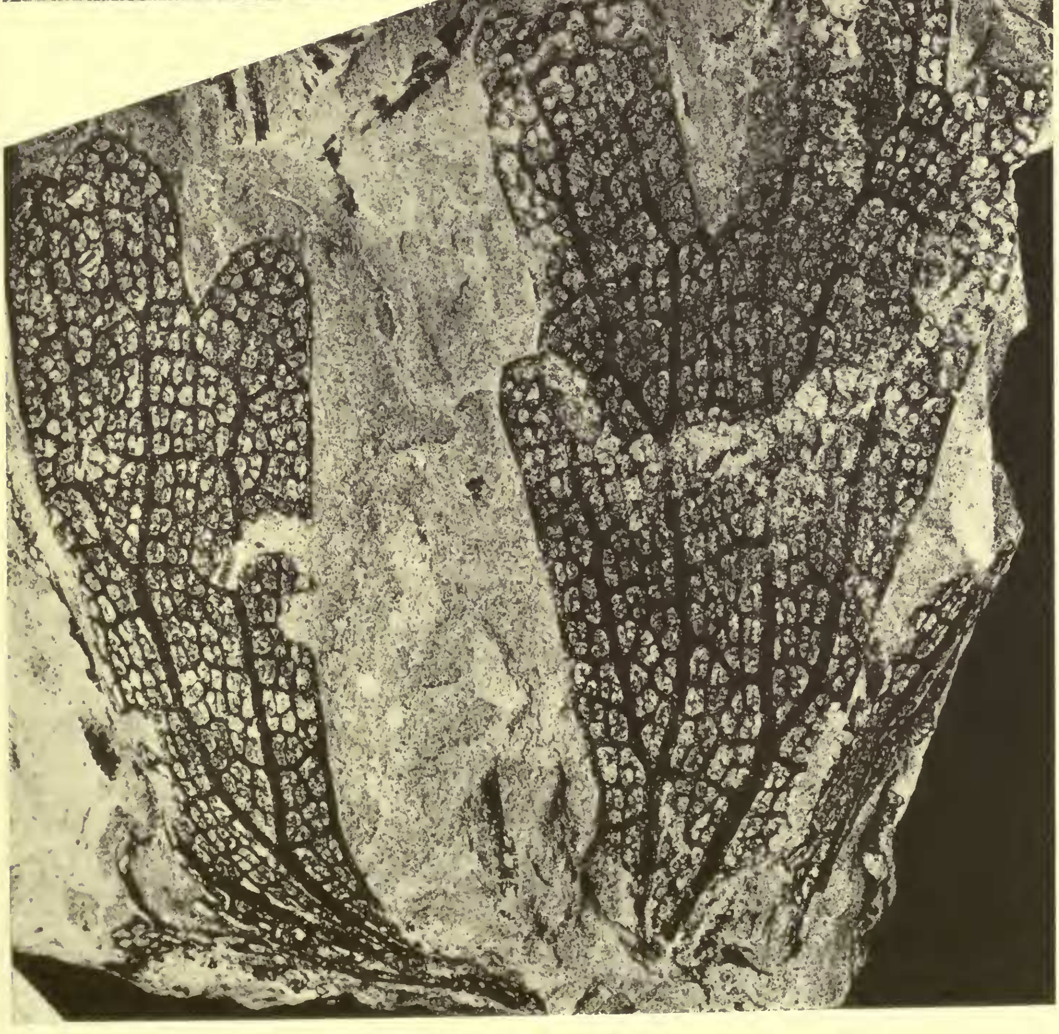


PLATE 4

Ruffordia goepperti (Dunker)

FIG. 1. Frond with narrowest form of segments. V.2157. × 1.

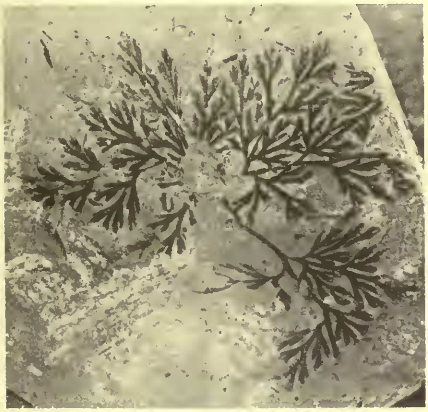
FIG. 2. Frond with wider sterile pinnules at the top. Fertile pinnae at the base scarcely visible (photographed dry). V.2295. × 1.

FIGS. 3, 4. Fronds with widest pinnules. Fig. 3, V.2357. ×1. Fig. 4, V.12331. ×1.

FIG. 5. Part of V.2157. × 3.

FIG. 6. Sterile part of V.2295. × 3.

FIG. 7. Pinna of V.2357 showing ventation. × 3.



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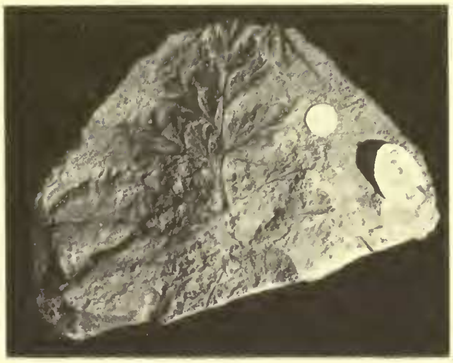

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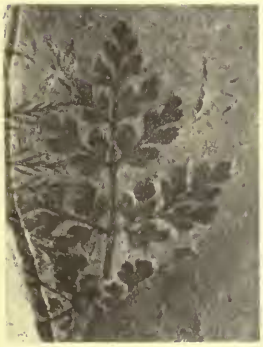

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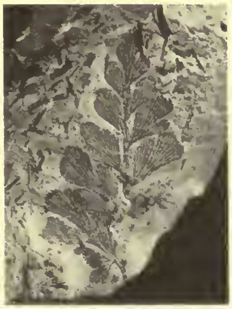

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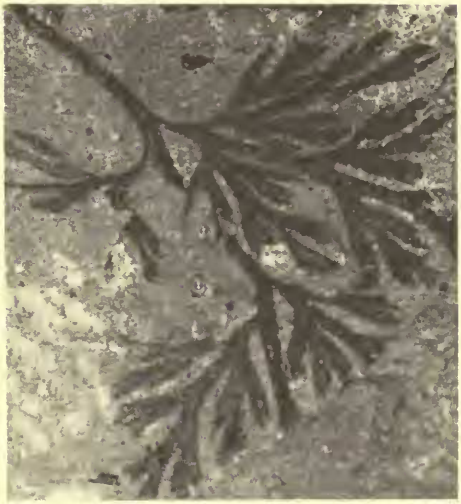

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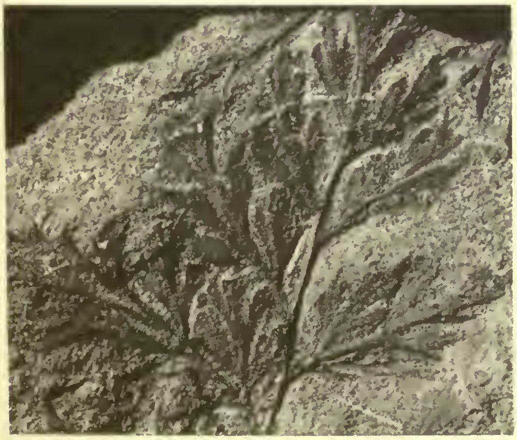

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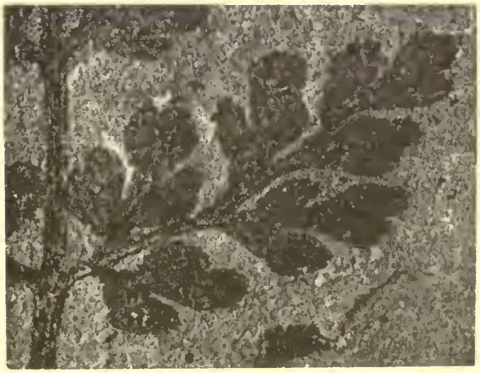

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PLATE 5

Ruffordia goepperti (Dunker)

FIG. 1. Specimen with sterile top and fertile base, immersed in paraffin. V.2295. × 1

FIG. 2. Fertile frond. V.2160. × 1.

FIG. 3. Fertile frond. V.2192*a*. × 1.

FIG. 4. Frond in Fig. 3 enlarged to show the undulating margins of the fertile pinnules. V.2192*a*. × 3.

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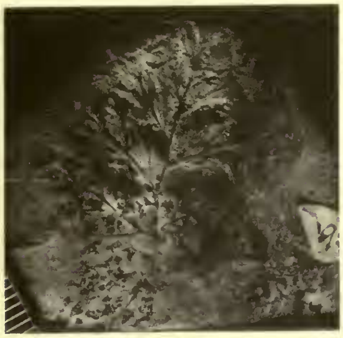

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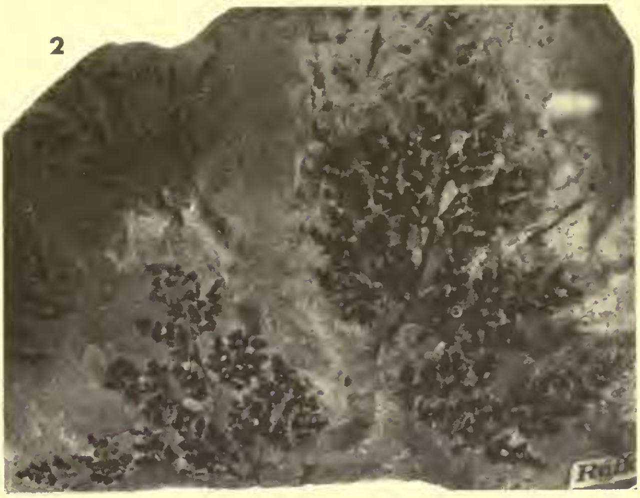

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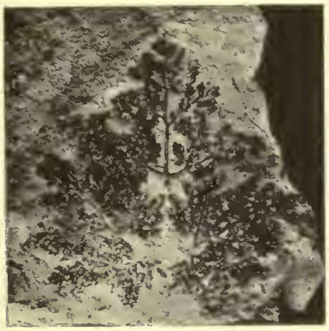

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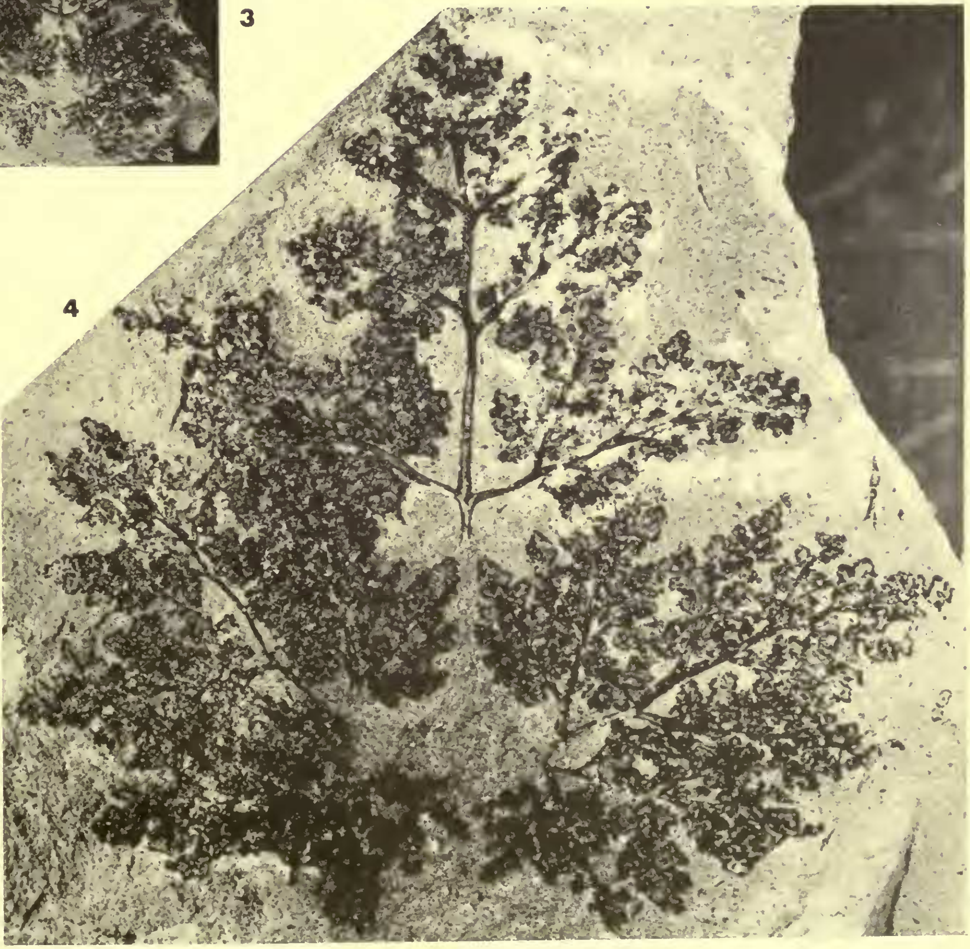


PLATE 6

Pelletieria valdensis Seward

FIGS. 1, 2. Largest fertile specimen picked out of the matrix. V.2368. Fig. 1, × 1, Fig. 2, × 3.

Aspidistes sewardi sp. nov.

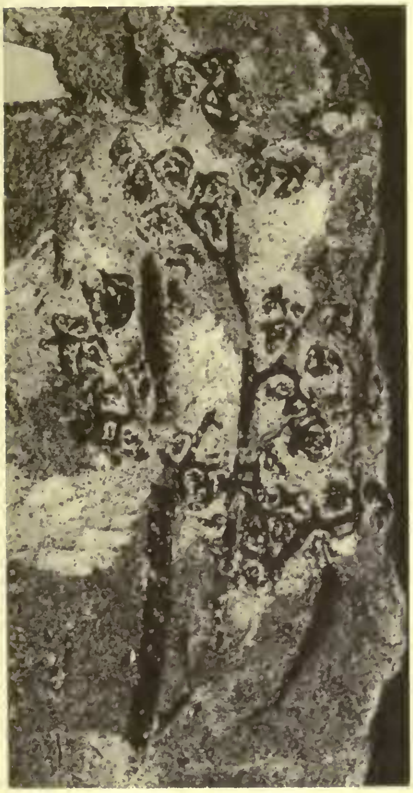
FIG. 3. Specimen immersed in paraffin, sori visible on most of pinnules. Holotype, V.2173*a* × 1.
FIG. 4. Middle part of same specimen enlarged to show rachis, sori and rolled edges. × 3.

Weichselia reticulata (Stokes & Webb)

FIG. 5. Part of pinna showing typical form with fleshy pinnules. Indication of reticulate venation just visible in two bottom-left pinnules. V.2174*a*. × 3.

Pseudotorellia heterophylla sp. nov.

FIG. 6. Cuticle of upper surface showing cells in " packets ", Geological Survey & Museum PF 2758, × 200.
FIG. 7. Cuticle of upper surface from same specimen showing sculptured surface of the cells, × 500.



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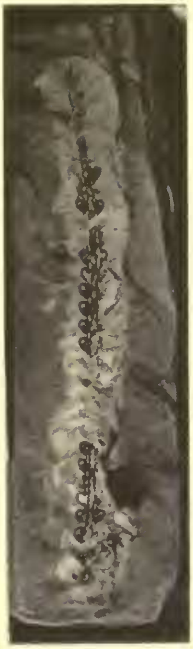

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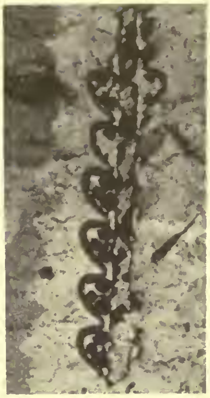

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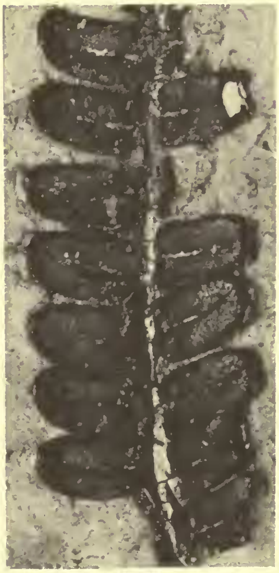

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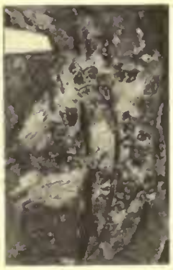

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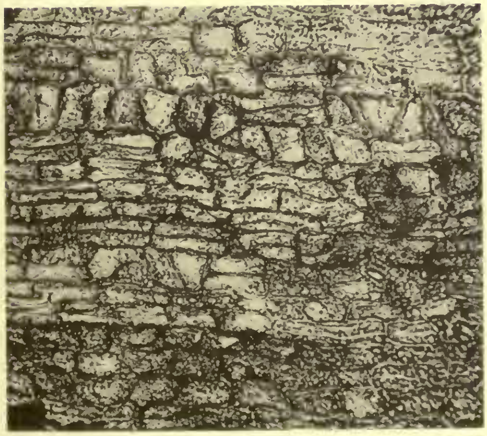

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